JOURNAL OF ANATOMY

ORIGINALLY THE JOURNAL OF ANATOMY AND PHYSIOLOGY

CONDUCTED ON BEHALF OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND BY

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LINCOLN'S-INN-FIELDS, LONDON, W.C.

VOLUME LIII

PARTS II AND III

APRIL 1919

Entered at New York Post Office as Second Class Matter

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CAMBRIDGE UNIVERSITY PRESS

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LONDON: FETTER LANE, E.C. 4

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THE DEVELOPMENT OF THE UROGENITAL SYSTEM IN THE MARSUPIALIA, WITH SPECIAL REFERENCE TO TRICHOSURUS VULPECULA

PART II

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INTRODUCTION

The following paper is the continuation of the study of the development of the urogenital system in marsupials, originally undertaken at the suggestion of Prof. J. P. Hill, to whom I am much indebted for constant advice. As in Part I, Trichosurus forms the basis for this investigation. The development of the rete and the urogenital connection was found to show considerable variation in different genera of both Monodelphian and Didelphian forms. These variations have been considered in some detail and form an interesting comparison with the conditions which have been observed in other Vertebrates. The development of the accessory glands relates exclusively to Trichosurus.

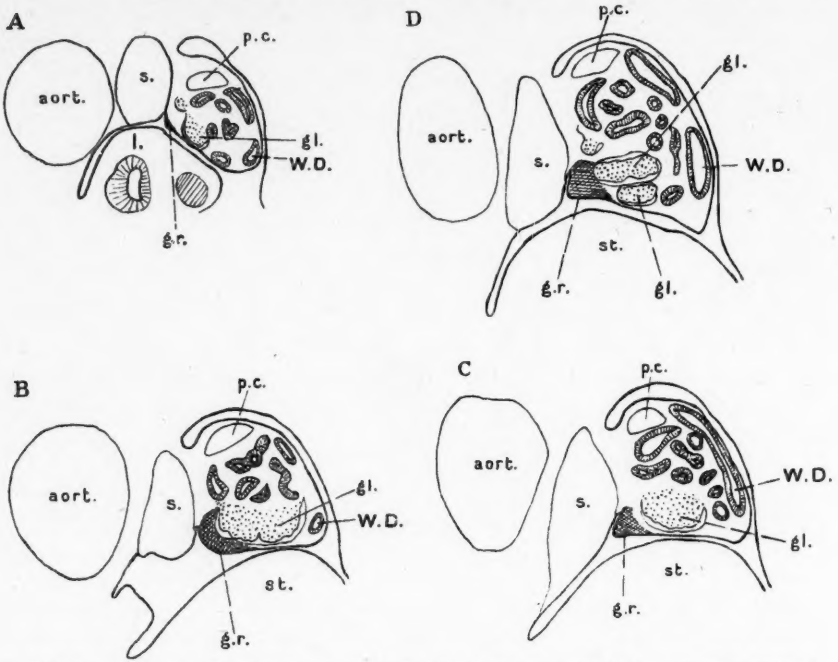
For the photomicrograph (text-fig. 12) of a transverse section through the cloacal glands, I have to thank Mr F. Pittock of the Zoological Department, University College.

GENITAL RIDGE AND DEVELOPMENT OF RETE

It is not easy to determine exactly at what stage the primordium of the genital organ first makes its appearance in Trichosurus. In an embryo of 7·5 mm. (Stage IV), however, a very low ridge can be seen, forming a slight projection into the coelom, along the medial side of the urogenital fold. The ridge is filled with denser cells, which at the cranial end, between the 7th

and 8th spinal ganglia, pass slightly dorsally, and eventually run into the cells forming the primordium of the suprarenal body, the latter at this level being situated just above the groove on the medial side of the urogenital fold. The posterior end of the ridge appears to reach almost as far as the 9th spinal ganglion.

In succeeding stages the genital primordium increases in length and becomes more prominent. By Stage VIII (*G.L.* 7·25 mm.) it appears as a



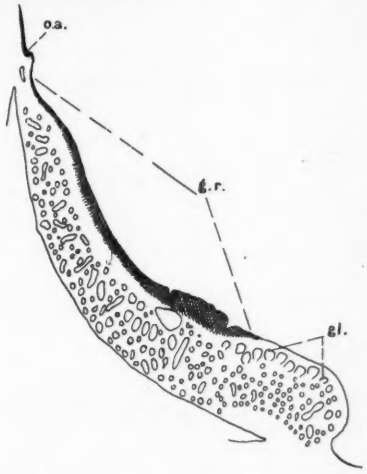
Text-fig. 1. *A, B, C, D. Trichosurus vulpecula. G.L.* 7·25 mm. (XII '02). Transverse sections through the urogenital fold, showing the genital ridge (*g.r.*) at different levels. *A* low anterior end of ridge; *D* well marked posterior end; *B* and *C* intermediate regions. *aort.* dorsal aorta; *gl.* glomerulus; *l.* lung; *p.c.* posterior cardinal vein; *s.* suprarenal body; *st.* stomach; *W.D.* Wolffian duct.

definite, though still low ridge (text-fig. 1, *A*, *g.r.*). It has now apparently become disconnected from the suprarenal organ, and gradually increases in thickness as it extends posteriorly (text-fig. 1, *B*, *g.r.*), its hinder portion forming a well marked elevation projecting out into the coelom (text-fig. 1, *C* and *D*, *g.r.*). The ridge is filled with a mass of darkly staining cells, which, on the inner side, lie close to the medial walls of the Malpighian corpuscles of the mesonephros.

Text-fig. 2 shows the genital ridge (*g.r.*) in an older embryo (*G.L.* 8·5 mm., Stage IX). The thicker posterior portion has a much indented margin, and

the tapering cranial end runs forwards almost as far as the ostium abdominale tubae (*o.a.*), but a definite connection with the latter does not seem to be established.

In embryos with a length of 11 mm. (Stage XII), the anterior portion of the ridge is more definitely marked out. As it extends forwards, it gradually passes from the dorso-medial side of the urogenital fold across the ventral surface of the mesentery, and on to the coelomic epithelium covering the suprarenal body. In this position it runs forwards as a small projecting ridge, triangular in section (text-fig. 3, *A*, *g.r.*), which in front of the mesonephros passes into the epithelium lining the shallow medial bay of the ostium abdominale (cf. Part I, fig. 19, *B*, *r.*).

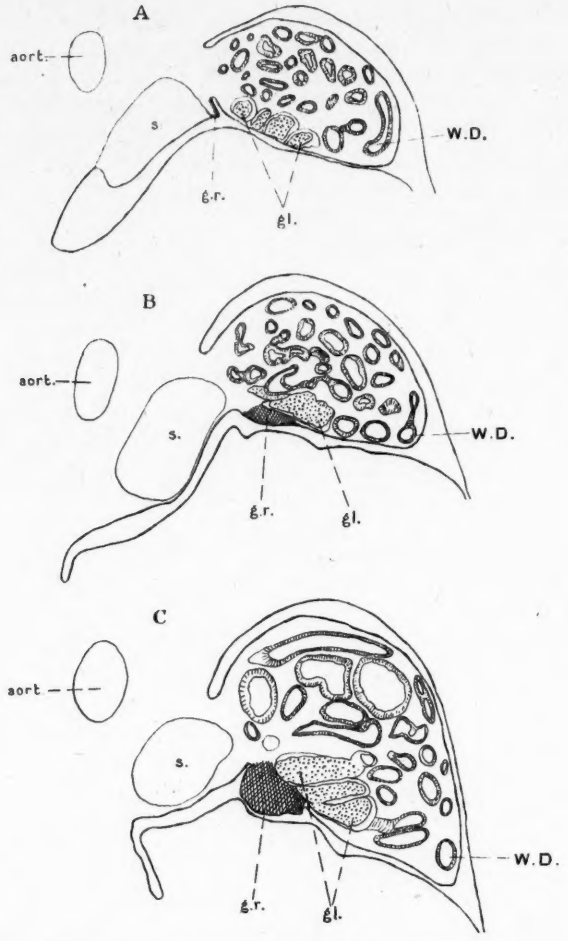


Text-fig. 2. *Trichosurus vulpecula*. *G.L.* 8·5 mm. ('97). Diagram of a longitudinal section of the mesonephros, showing the genital ridge (*g.r.*) lying along the ventro-medial side of the urogenital fold. *gl.* glomeruli; *o.a.* ostium abdominale.

The posterior part of the ridge (text-fig. 3, *C*, *g.r.*) is becoming very conspicuous, and by Stage XIV (*G.L.* 13 mm.) it is already differentiating into the future gonad. The differentiation is, however, very slight, although primitive sex cells are now distinguishable for the first time. The primordium of the gland is also becoming more divided off from the mesonephros, although a mesogenitale is not yet developed.

Just before birth (*G.L.* 14 mm.) the cells within that part of the ridge situated in front of the primordium of the definitive gonad have become concentrated to form a core of deeply staining cells, which extends from the ostium abdominale all along the ridge into the hilum of the genital organ. This core is the primordium of the rete, and that part of the ridge, within which it lies, may now be termed the rete ridge. In early stages, the rete ridge is simply the reduced anterior continuation of the genital ridge; it is

identical with the latter and cannot be distinguished from it, the one gradually passing into the other.



Text-fig. 3. *Trichosurus vulpecula*. *G.L.* 11·5 mm. (VII '01). Transverse sections through the mesonephros showing the genital ridge (*g.r.*) at different levels. *A* near the anterior end of the mesonephros, where the genital ridge forms a small projection close to the suprarenal body (*s.*); *B* further posteriorly; *C* thicker posterior portion of ridge. *aort.* dorsal aorta; *gl.* glomeruli; *s.* suprarenal body; *W.D.* Wolffian duct.

In pouch young with a head length of 7·5 mm., these two regions are more definitely marked out. The rete, which is now composed of irregular cords and strands of cells, extends from the ostium abdominale, between the 19th

and 20th spinal ganglia, to just behind the 21st spinal ganglion, where it runs into the gonad. The latter is now connected with the Wolffian body by a short thick mesogenitale, whilst a bundle of small arteries and veins, related to the dorsal aorta and the vena cava respectively, passes down along the medial border of the urogenital fold, through the mesogenitale into the genital gland. This vascular bundle, together with a branch from the sympathetic system, forms a conspicuous formation in later stages, running through the mesogenitale on the posterior side of the rete.

In pouch young of this age (*H.L.* 6·75 to 8 mm.), and again in later stages, definite ingrowths, in the form of hollow invaginations (Pl. VII, fig. 3) and solid cords, are to be seen extending inwards from the coelomic epithelium of the rete ridge, to merge at their inner ends with the cell strands of the rete itself. It must be noted that in late embryos, before the formation of the rete core, the ridge is indented (*G.L.* 11 mm., Pl. VII, fig. 1) by more or less distinct grooves extending in from the coelomic epithelium (*G.L.* 14 mm., Pl. VII, fig. 2), but it was not possible to determine whether these ingrowths are actually connected with the development of the rete, as are the more definite invaginations present in early pouch young. Shortly before birth, comparable ingrowths from the coelomic epithelium of the gonad were first observed passing inwards into the substance of the latter.

Having traced the early development of the genital ridge and its differentiation into gonad and rete, the further development of the latter and the establishment of the urogenital connection must be considered in conjunction with the degeneration of the mesonephros.

DEGENERATION OF MESONEPHROS AND FORMATION OF UROGENITAL CONNECTION

In Part I of this paper the development of the mesonephros was followed from comparatively early embryos up to pouch young with a head length of 7·5 mm., at which time it was still a fully developed organ. In a male foetus with a head length of 8 mm. (*G.L.* 18 mm.), we find that the mesonephros has entered on a new and final phase of its history. Degenerative changes first occur at the anterior end. At this end, on the left side, is a small atrophied tubule, quite isolated, and behind it, the next few tubules are narrow and darkly staining. They have a uniform appearance throughout their length, and are already surrounded by much connective tissue. They run dorsally into the Wolffian duct, but the connection with their Malpighian corpuscles, which are small and in process of degeneration, was not very distinct in this foetus. A short distance further back (about ·096 mm.) normal secretory tubules make their appearance, and continue throughout the remainder of the mesonephros, which is well developed and apparently functional. On the right side, the degenerate portion is slightly shorter.

The rete ridge lies along the medial side of the Wolffian body, gradually increasing in size as it approaches the testis. Within the ridge, the primor-

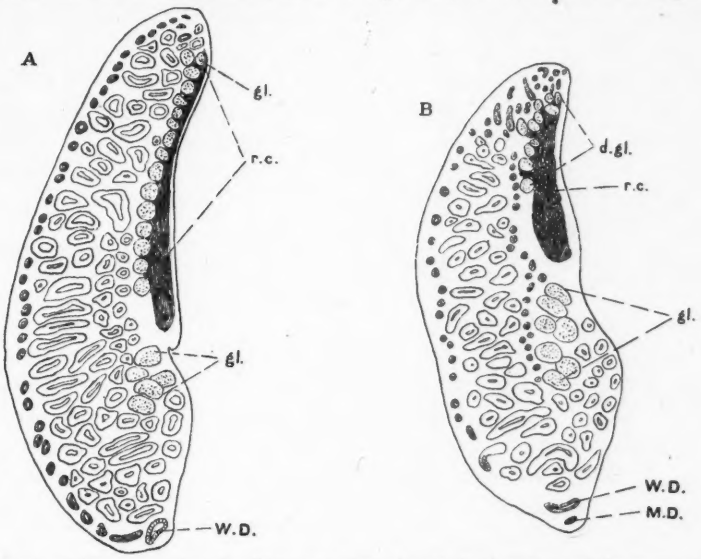
dium of the rete is composed of irregular cords and strands of darkly staining cells, which, in this foetus, a male, are in close connection with the seminiferous tubules, whilst in a female of nearly the same age, they run into the central mass of the ovary. At the anterior end of the mesonephros, some of the rete cords bend slightly inwards to terminate close to the small anterior degenerating Malpighian corpuscles, and further posteriorly, down to about the 15th glomerulus, strands of cells pass from the rete up to the walls of Bowman's capsules. Although these strands do not appear to be definitely attached to the walls of the capsules in this foetus, such a connection is already present in a female with a head length of 7·5 mm. (*G.L.* 14·75), opposite the 13th glomerulus.

In a pouch young with a head length of 8·5 mm. (*G.L.* 20 mm.), similar degenerative changes are again seen in the mesonephros. At the anterior end of the urogenital fold are a few isolated tubular fragments, and behind these, we find a small number of anastomosing canals with darkly staining walls, each surrounded by several circular layers of connective tissue. The former secretory portions of the tubules, adjoining the Malpighian corpuscles, have now quite lost their characteristic structure. The first transformed secretory tubules of this stage appear to have already lost their glomeruli. A short distance posteriorly, unchanged secretory tubules appear, and connected with them are well formed glomeruli. On the right side, the mesonephros is fully developed almost up to the extreme anterior end, and it has altogether a length of 1·53 mm. The posterior tubules on each side are large, with marked Malpighian corpuscles, the latter having approximately the same diameter as those in pouch young with a head length of 7·5 mm. (cf. Part I). The rete has the same relations as in the last stage (*H.L.* 8 mm.).

In pouch young with a head length of 9 mm., both ♂ and ♀, the involution of the mesonephros is more marked, the anterior portion of the gland having shrunk considerably, whilst the rete has also undergone a corresponding shortening. Text-fig. 4, *A* and *B*, shows the reduction in length which occurs between a foetus with a head length of 7·5 mm. (*A*) and one of 9 mm. (*B*). At its extreme anterior end, the rete lies close to the walls of the degenerating Malpighian corpuscles (Pl. VII, fig. 4, *r.c.*), whilst more posteriorly, it is further removed from these, and sprouts extend out from it to unite with their walls.

At 11 and 12 mm. head length, presexual and postsexual regions, as described by von Winiwarter and Sainmont ('08), are definitely marked out in the mesonephros, but the transition between the parts is a gradual one, the intermediate or sexual region lying opposite the reproductive gland. The entire organ is now bent round, so that the presexual region, destined to give rise to the epididymis in the male and to the epoophoron in the female, lies dorso-medially, and partly anterior to the postsexual portion, and dorso-laterally to the testis or ovary. The anterior end of the Wolffian duct is wide and curves round medially; from it arise rows of narrow darkly staining tubules, which run down ventrally and are surrounded by layers of con-

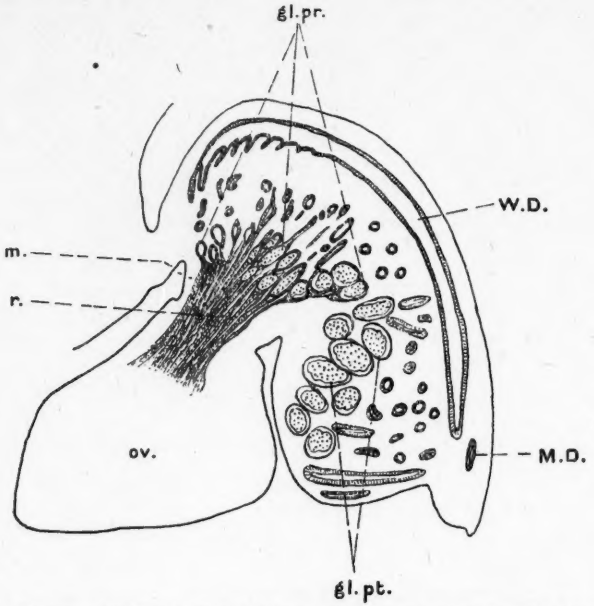
nective tissue. Some are of greater diameter and have larger lumina than others, but all have thin walls, and have quite lost the characteristics of secretory tubules. The glomeruli opposite the anterior end of the rete are very small, but they increase in size posteriorly, and are quite large at the beginning of the sexual region. The rete runs through the genital mesentery and its darkly staining twisted strands, in some of which the cells are beginning to take on a radial arrangement, are united with the walls of the Malpighian corpuscles. This union appears usually to take place before the actual degeneration of the glomeruli, as it is especially well seen in the larger un-



Text-fig. 4. *Trichosurus vulpecula.* Diagrams of two longitudinal sections of the mesonephros, *A* 7·5 mm. *H.L.*, *B* 9 mm. *H.L.*, showing the shortening of the anterior end of the mesonephros and of the rete (*r.c.*) between the two stages. Both drawn to the same scale. *d.gl.* anterior degenerating glomeruli; *gl.* glomeruli; *M.D.* Müllerian duct; *W.D.* Wolffian duct.

changed corpuscles, which lie in the postero-lateral portion of the sexual region (Pl. VIII, fig. 5, *spr.*). Whether the walls of the Malpighian corpuscles give rise to definite outgrowths, which extend towards and unite with the rete cords, was not definitely determined, but from the appearances presented in this stage I have reason to believe that such outgrowths are developed (Pl. VIII, fig. 5, *spr. gl.*). In any case, however, they must only be short, as the main connection is evidently supplied by sprouts from the rete cords themselves. In the sexual region the tubules are found to be in all stages of degeneration. The postsexual region is still well developed and functional; it lies ventro-laterally to the reproductive gland, its anterior end appearing in the same transverse sections as the presexual portion, and, being cut longitudinally, six or seven glomeruli appear in one section.

In pouch young with a head length of 12·5 mm. (♀), the presexual portion has widened dorso-ventrally, owing apparently to increase of connective tissue. In the presexual region, some of the Malpighian corpuscles have become narrow, and present a drawn-out appearance (text-fig. 5), whilst a few seem to have completely disappeared, so that the strands of the rete are directly connected with the narrow tubules, and by them with the Wolffian



Text-fig. 5. *Trichosurus vulpecula*. *H.L.* 12·5 mm. Transverse section through the mesonephros and ovary, showing the mass of rete strands (*r.*), which extend from the walls of the Malpighian corpuscles (*gl.pr.*) of the presexual region of the mesonephros, through the mesovarium (*m.*) into the ovary (*ov.*). The glomeruli are seen to be in progressive stages of degeneration. *gl.pt.* glomeruli of postsexual region of mesonephros; *M.D.* Müllerian duct; *W.D.* Wolffian duct.

duct. At the posterior end of the sexual region there is much connective tissue, and degeneration of the secretory tubules is proceeding actively. The same changes as have been described in the presexual region are now occurring at the anterior end of the postsexual portion, where the glomeruli are small, but further posteriorly the gland evidently still functions, and the glomeruli are large. On the left side, the disposition of the different regions is like that of the last stage, but on the right the bending of the mesonephros is not so marked, the postsexual portion lying posterior to the presexual.

EPOOPHORON AND PAROOPHORON

In the female in later stages, from a head length of 15 mm. up to a head length of 24 mm., a gradual degeneration of the presexual portion or epoophoron occurs. The connective tissue becomes abundant, and the tubules, although retaining their connection with the rete, become detached from the Wolffian duct, which degenerates. The tubules gradually decrease in number, and degenerating glomeruli are present. In the oldest foetus (*H.L.* 38 mm.), the epoophoron consists of a group of small, mostly hollow tubes, some of which run into the rete. The rete, which becomes distinctly tubular in the foetus with a head length of 15 mm., remains well marked, much more so than in the male of the same age; the cords become thick and darkly staining, with well developed lumina, and, as in earlier stages, they extend into the centre of the ovary. Later, cavities and spaces appear to develop in it.

The paroophoron, which is derived from the postsexual portion of the mesonephros, undergoes a similar degeneration to the epoophoron, but the process is carried still further. In the foetus with a head length of 24 mm., it consists of a few narrow tubes and several degenerating Malpighian corpuscles, and into it runs a large nerve from the sympathetic system. Finally, in older stages, only a few tubular remnants remain.

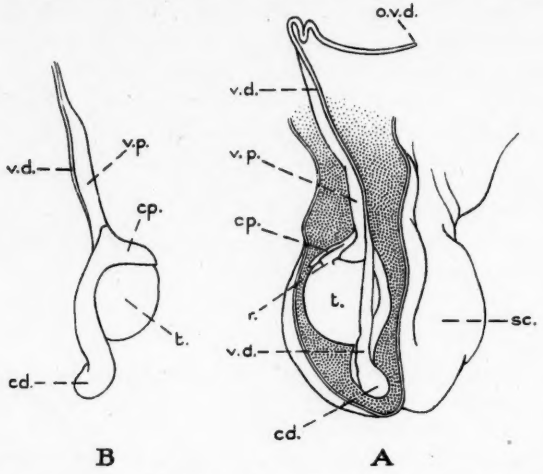
EPIDIDYMIS AND PARADIDYMIS

In a male with a head length of 15 mm., the epididymis, which like the epoophoron represents the presexual part of the mesonephros, is quite a distinct structure, and consists of a collection of darkly staining tubules lying dorso-laterally to the testis, and running into the Wolffian duct. They are connected with the rete strands, which are now becoming tubular, and which extend into the mesorchium to unite with the seminiferous tubules. In the postsexual portion, destined to become the paradidymis, degeneration of the tubules is seen throughout its extent. They are narrow and resemble those of the epididymis, but are not so darkly staining as the latter. Though fairly large glomeruli are present at the posterior end, the gland is obviously no longer functional.

In a male with a head length of 20 mm. the epididymis has begun to descend with the testis, and lies with the latter a short distance anterior to the scrotal sac in the saccus vaginalis on the ventro-lateral side of the body. It is composed of many fine tubules connected with the Wolffian duct, and is surrounded by investing layers of connective tissue. The tubules dilate slightly where they pass into the rete, at the point where the former Malpighian corpuscles were situated. The rete is poorly developed, being less marked than in the foetus of 15 mm. *H.L.*, or in the female with a head length of 24 mm., and is composed of fine tubes or strands of cells. In a pouch young of 26 mm. *H.L.*, the epididymis is a conspicuous mass of coiled tubules with darkly staining walls, lying on the dorsal side of the testis; the tubules run

into the Wolffian duct. The latter is now coiled on leaving the epididymis to form the vas deferens. The rete consists of a small bundle of very fine tubules, which pass from the canals of the epididymis through the mesorchium to be connected with the seminiferous tubules at the base of the testis.

In the adult, the epididymis (text-fig. 6) is divided into a caput (*cp.*), which overlies the dorsal side of the testis, and a cauda (*cd.*), the two portions being united by means of an elongated narrow part running along the medial border of the gonad. The cauda projects beyond the testis as a bulbous mass,



Text-fig. 6. *Trichosurus vulpecula.* Adult. *A.* Dissection of the scrotal sac, showing the testis and the epididymis of the left side. Anterior view. *B.* Posterior view of testis and epididymis. *cp.* caput epididymis; *cd.* cauda epididymis; *o.v.d.* opening of vas deferens into urethra; *r.* rete testis; *sc.* scrotum; *t.* testis; *v.d.* vas deferens; *v.p.* vascular plexus.

and is connected with the scrotal sac by a short gubernaculum. A short narrow rete (*r.*) runs from the genital gland into the caput of the epididymis.

The degeneration of the paradidymis resembles that of the paroophoron. It consists, in the male with a head length of 26 mm., of a few tubules disconnected from the Wolffian duct and surrounded by much connective tissue. It lies ventrally and posteriorly to the epididymis, and is united with the latter by a broad mesentery, whilst more posteriorly it is joined to the very narrow mesorchium.

SUMMARY

In early stages of Trichosurus, the primordium of the gonad and rete first appears as a low ridge, which projects into the coelom on the medial side of the urogenital fold. The ridge is filled with slightly denser cells, which are not sharply marked off from the adjacent mesenchyme. Anteriorly, these cells are at first continuous with the primordium of the suprarenal

body, but, in the next few stages, the cranial end of the ridge is less distinct and difficult to follow; in older embryos (*G.L.* 11 mm.), however, up to the involution of the mesonephros, the epithelium of the ridge can be traced forwards into continuity with that of the ostium abdominale, and the connection with the suprarenal organ is lost. The ridge gradually increases in thickness towards the posterior end, and, shortly before birth, it becomes distinctly differentiated into two portions, an anterior one, forming the rete ridge, and a posterior, representing the primordium of the gonad. Within the rete ridge lies a deeply staining core of cells, the rete core, which extends from the ostium abdominale into the genital gland. For some time before birth, before the formation of the rete core, groove-like invaginations of the coelomic epithelium are to be seen in the region of the rete ridge, but it is only in pouch young with a head length of 6·75 mm. and in following stages, that actual cords of cells are to be observed connecting the coelomic epithelium with the rete core. The latter comes to consist of irregular cords and strands of cells which, in pouch young with a head length of 15 mm., assume a tubular structure, constituting the definitive rete canals.

The involution of the mesonephros sets in in pouch young with a head length of 8 mm. At this time, the cranial end of the rete primordium lies close against the walls of the anterior degenerating Malpighian corpuscles, but more posteriorly it is further removed from the latter, and by means of sprouts from the rete cords definite connections with the walls of Bowman's capsules are now established. Short outgrowths also seem to be developed from the walls of the latter, but these take a very insignificant part in the formation of the urogenital connection. The changes at the cranial end of the mesonephros are at first precisely similar in both sexes. One or two of the most anterior tubules probably disappear completely. In the following seventeen or eighteen, the secretory portions of the tubules lose their characteristic structure, and take on the appearance of collecting tubules, whilst the Malpighian corpuscles gradually undergo transformation, their glomeruli disappear, their walls thicken, and, after the connection with the rete is established, they become reduced to short uniformly narrow tubes, in continuity with, and of the same diameter as the altered secretory portions of the tubules. During this transformation, the connective tissue round the tubules increases in amount, and the whole anterior end of the mesonephros undergoes considerable shrinkage. The degenerating corpuscles are drawn closer together, and the rete, being attached to the latter, becomes correspondingly shortened in antero-posterior extent. This anterior or presexual portion of the mesonephros is destined to develop into the epididymis in the male and the epoophoron in the female. In the male, the tubules retain their connection with the Wolffian duct which becomes the vas deferens. They come to consist of a mass of coiled and darkly staining canals, the canals of the epididymis, which communicate with the seminiferous tubules by a bundle of fine rete tubes or vasa efferentia running through the mesorchium.

The urogenital connection in Trichosurus thus involves a large number of rete canals, and 17 or 18 mesonephric tubules, the latter giving rise to the epididymis (text-fig. 8, *A*).

In the female with a head length of 15 mm., and in later stages, the presexual portion or epoophoron gradually deteriorates, the degenerating tubules become detached from the Wolffian duct and eventually atrophy. The rete, on the other hand, appears to remain well marked, even in later stages, where it forms a conspicuous mass of narrow canals, which stretch from the centre of the ovary right through the mesovarium, terminating blindly at both ends.

The degeneration of the posterior portion of the mesonephros begins in pouch young with a head length of about 11 mm. The secretory portions of the tubules break down and the glomeruli degenerate. The atrophy, which begins in the sexual portion of the gland, gradually spreads to the postsexual region, until finally only vestiges of tubules and glomeruli remain. These form the paradidymis in the male and paroophoron in the female. The former completely disappears, whilst the latter, in older females, consists of only a few tubular remnants.

THE UROGENITAL CONNECTION IN OTHER MARSUPIALS

The only detailed observations on the rete and urogenital connection of marsupials are those of van den Broek. In a paper on the female urogenital organs, this author ('05) describes and figures a larger or smaller number of branching and anastomosing rete canals in the hilum of the ovary of an adult *Petrogale penicillata*. These canals were isolated and had no connection with any other structures, and from their appearance van den Broek suggests that they may possibly be a new formation. It may be noted that, in 1901, Berry Hart ('01) pointed out the occurrence of a canalicular system at the hilum of the ovary in the rat kangaroo. This was continuous with the epoophoron and was therefore considered as representing the paroophoron.

In the male pouch young of Dasyurus (*D.C.L.* 53 mm.), van den Broek ('07) has shown that the seminiferous tubules unite into a single duct, which runs through the mesorchium, then coils to form the epididymis, and finally passes back as the vas deferens. In a female with a length of 40 mm. (*D.C.L.*), the cranial end of the Wolffian duct is described as passing through the mesovarium into the hilum of the ovary. In older females (*D.C.L.* 53 and 63 mm.), he found that the anterior end of this duct was simply a blind canal lying near the hilum. From these observations van den Broek comes to the conclusion that the cranial end of the Wolffian duct in both sexes grows through the mesentery into the base of the genital gland, forming the pars conjunctiva in the male and remaining in the female of later stages as an isolated duct. He states that the mesonephros atrophies completely, and that in the male the canals of the epididymis or pars conglomerata arise by sprouting, or

more probably by division of the primitively single Wolffian duct. According to him, no rete is developed. The conditions in Didelphys point, he says, to a similar conclusion. In male pouch young of Didelphys spec. (*D.C.L.* 102 and 130 mm.), and also in a full-grown *D. virginiana*, a single canal passes from the tubules of the testis through the mesorchium, and divides into the many canals of the epididymis. In a later communication van den Broek ('10, *a* and *b*) states that the same conditions are present in the Phalangeridae and Macropodinae, and that here also there is at first only a single duct from which the canals of the epididymis later arise. This author therefore supposes that the urogenital connection in marsupials has a widely different origin from that of other mammals.

From our observations on Trichosurus, it is evident that the conditions described by van den Broek do not hold for all marsupials. Van den Broek, however, had little or no opportunity of examining embryos or early pouch young, and his conclusions are based on the examination of comparatively late stages. From the unique collection of early stages in the possession of Prof. J. P. Hill, I have been able to investigate a complete series of early pouch young of Dasyurus, also early Didelphys, besides several stages of other forms. It is of some interest to compare these observations with those of van den Broek, and with the conditions already described in Trichosurus.

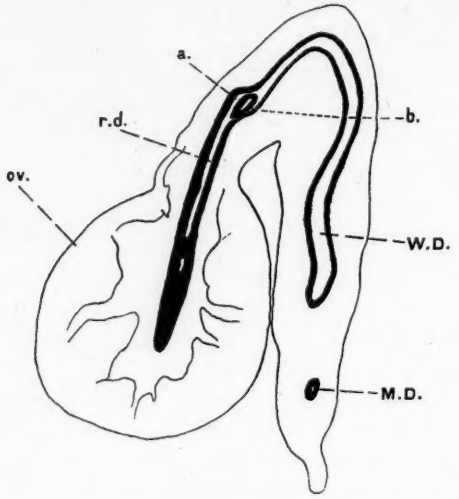
POLYPROTODONTIA

Dasyurus viverrinus. In very early pouch young of Dasyurus (*H.L.* 3 to 4 mm., Stages C and D) the rete ridge has the same relations as in embryos of Trichosurus. It passes back from the medial side of the ostium abdominale as a low ridge, which increases in size as it continues posteriorly into the gonad. Within the ridge is a concentration of cells, but as yet no definite cord has developed. At the next stage (*H.L.* 4·5 to 5·5 mm., Stages E and F), from the posterior wall of the ostium abdominale a short tubular groove extends inwards and continues back as a solid and distinct cord of cells, the rete cord, which runs on the inner side of the rete ridge, close to the walls of the Malpighian corpuscles. Near the gonad, the cord becomes thicker, and finally, after passing through the mesentery, runs for a short distance into the gland, where it either ends blindly or is intimately connected with the central cells of the latter. The Müllerian duct at this stage extends back as far as the posterior end of the mesonephros.

In pouch young with a head length of 6·5 to 8 mm. (Stages G and H), the rete cord in both sexes is becoming transformed into a definite tubular duct. This rete duct runs out from the reproductive gland through the mesentery and along the rete ridge, where it passes very close against the walls of the Malpighian corpuscles of the mesonephros. Further cranially, the duct moves slightly dorsally, out of the rete ridge, and, at the anterior end of the excretory gland, it turns laterally and becomes connected with the cranial end of the Wolffian duct by two, or sometimes possibly three,

narrow tubules; these most probably represent the two most anterior mesonephric tubules, which, with their glomeruli, have already undergone transformation. Apart from the union of these two tubules with the rete duct, there is as yet no differentiation at the anterior end of the mesonephros, and the rete ridge itself passes as before into the posterior side of the ostium abdominale.

At the next stage (*H.L.* 10 and 10·5 mm., Stage I), there is marked atrophy at the cranial end of the mesonephros. Much connective tissue is present, the glomeruli are undergoing degeneration, whilst the collecting tubules are breaking down and are apparently no longer connected with the Wolffian duct. At the posterior end, the mesonephros is still well developed,



Text-fig. 7. *Dasyurus viverrinus*. *H.L.* 12 mm. (About J). ♀. Diagram of a transverse section of the ovary and anterior end of the Wolffian duct. The single rete duct (*r.d.*) passes out from the centre of the ovary (*ov.*) and is united with the Wolffian duct (*W.D.*) by two tubes, a larger (*a*) and a narrower (*b*), which probably represent the most anterior tubules of the mesonephros. *M.D.* Müllerian duct.

as are the Malpighian corpuscles. In the male, the seminiferous tubules are for the most part tubular. They unite towards the base of the testis into a solid cord of cells, which soon becomes hollow as it passes through the mesorchium. The rete duct thus formed, shortly after leaving the mesorchium and behind its connection[1] with the Wolffian duct, buds off many small tubules, some of them mere short culs-de-sac. These tubules continue into the degenerate mass at the anterior end of the excretory organ, and may perhaps represent the sprouts which formerly connected the rete with the Malpighian corpuscles, now completely atrophied. The appearances at this

[1] It was impossible to determine in this foetus whether this involved one or two tubules.

stage point to an abortive attempt on the part of the rete to become attached to the mesonephric tubules, such as occur in the formation of the epididymis in Trichosurus.

In a male with a head length of 11·5 mm. (Stage J), the mesonephros is quite degenerate, even at the posterior end. The cranial portion is simply a mass of connective tissue with remnants of tubules, but more posteriorly remains of secretory tubules and degenerating glomeruli can be recognised. The condition of the rete duct is similar to that of the last stage, but in a slightly older female (*H.L.* 12 mm.) it is connected with the Wolffian duct by two distinct tubules (text-fig. 7), whilst in one with a head length of 12·5 mm. the anterior end of the Wolffian duct has disappeared, the rete duct simply becoming dismembered at its cranial end.

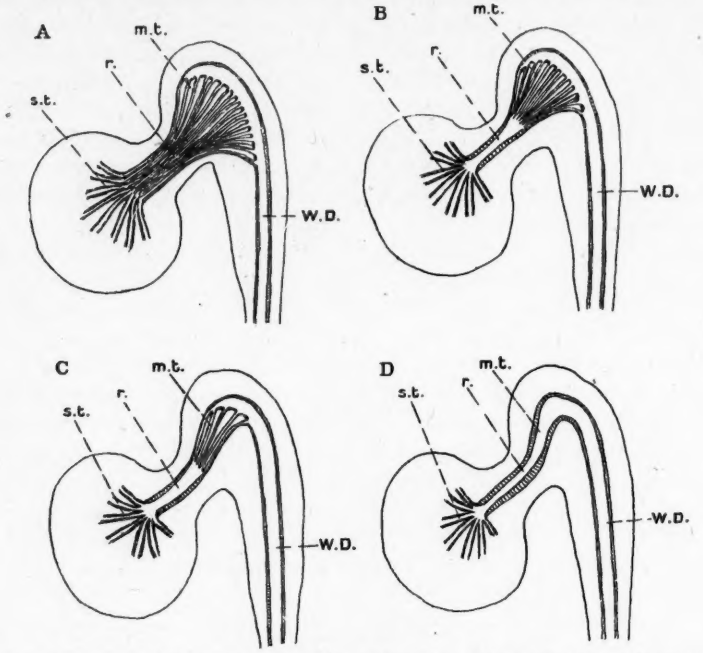
In females with a head length of 18 and 22·5 mm. (Stages K and L) the rete duct arises from the ovary, and passes through the mesovarium as a conspicuous tube with a large cavity and darkly staining epithelial walls. It becomes reduced in size and disappears soon after leaving the mesovarium.

In a male with a head length of 18 mm., the testes have begun their descent, and lie close to the ventral wall of the abdomen on each side, just cranially to the scrotal sac. The seminiferous tubules, towards the base of the testis, unite into a single duct, which, passing through the mesorchium, becomes much narrower in diameter, and runs forwards and slightly dorsally to become continuous with the vas deferens. From the conditions in the female shown in text-fig. 7, it is clear that either the two anterior tubules of the mesonephros there present, coalesce to form one tube, or that one of them disappears. In an older male (*H.L.* 22·5 mm., Stage L), the rete duct, after leaving the mesorchium, continues as a single tube, which, coiling round in a connective tissue basis, forms the primordium of the epididymis, and runs into the vas deferens. In a still older stage (*H.L.* 3·6 cm., Stage N), a distinct epididymis is present. It is a tubular structure, lying in connective tissue, and is divided into a caput and a smaller cauda, the two united by a narrow intermediate portion. Certainly in the cauda, and most probably also in the caput, the gland is composed of a single, much convoluted tube, developed by coiling from the single duct. How much of this duct corresponds to the mesonephric tubule originally connecting the rete and Wolffian ducts, and how much is derived from the anterior end of the Wolffian duct alone, it is impossible to ascertain. Whether in late stages there is any branching of the originally single duct into many tubules, as suggested by van den Broek, I have not been able to determine.

The urogenital connection in Dasyurus is thus composed of a single rete canal and one or two mesonephric tubules (text-fig. 8, *D*).

Didelphys. The pouch young of Didelphys consisted of males of *D. aurita* with a head length of 8, 9, 10·5, 12, 18 and 20 mm., and two females with a head length of 9·5 and 18 mm. respectively. Observations were also made on a male of *Metachirus opossum* of 13 mm. *H.L.*

In the earliest stage (*H.L.* 8 mm.) there is only a slight indication of degeneration at the anterior end of the mesonephros. The rete ridge is well marked. It arises from the medial bay of the ostium abdominale, and extends back, increasing greatly in size, along the medial side of the urogenital fold. The anterior region is filled with masses of darkly staining cells, which, more posteriorly, are connected into a single cord. This cord becomes a duct as it passes into the mesorchium, and finally unites with the seminiferous tubules. At a few places along the ridge, solid cell cords extend from the coelomic



Text-fig. 8. Diagrams illustrating the condition of the rete and mode of origin of the epididymis in different marsupials. *A*. Trichosurus. *B*. Didelphys. C. Perameles. *D*. Dasyurus. *m.t.* transformed mesonephric tubules destined to form epididymis; *r.* rete; *s.t.* seminiferous tubules; *W.D.* Wolffian duct.

epithelium into the rete core, in the same manner as described and figured for Trichosurus. These ingrowths are still more marked in the next foetus (*H.L.* 9 and 9·5 mm.), and are also present along the mesogenitale. At this stage the rete ridge is very prominent, and within it the rete forms a cord of darkly staining cells. The secretory portions of the most anterior tubules of the mesonephros are no longer recognisable, and, on the right side in the male, the first five glomeruli lie close together, and from the ventral walls of their capsules a thick solid cord of cells stretches ventrally and posteriorly into the rete cord. The latter is also becoming attached to the more posterior

Malpighian corpuscles. On the left side, the most anterior degenerate glomerulus appears to be isolated, whilst behind it three are united with the rete as are the first five on the right.

In the next male (*H.L.* 10·5 mm.), the connection of the rete, which is now becoming a definite duct, with the five anterior transformed tubules of the mesonephros is well seen, especially on the right side (Pl. VIII, fig. 6). The first tubule (*t.* 1) now consists of a narrow duct running into the Wolffian duct dorsally, and united on the ventral side with the rete; its glomerulus has entirely disappeared. In the second tubule, the position of the former glomerulus (*gl.* 2) is marked by a slight swelling of the tube and a thickening of its walls at this point. The other glomeruli (*gl.* 3, 4, and 5) are seen to be in progressive stages of degeneration. In this foetus, at the base of the right testis, the coelomic epithelium is connected with the rete duct by strands of cells. At an older stage (*H.L.* 12·5 mm.), eleven transformed mesonephric tubules (possibly twelve on the right side) are united with the rete duct ventrally, and run up dorsally into the Wolffian duct, the portion connecting them with the latter having thinner, more lightly staining walls. Definite Malpighian corpuscles are only recognisable in connection with the hindermost of these tubules. This region is destined to form the epididymis; behind it, on both sides, there is a zone of degenerate glomeruli and tubules, surrounded by much connective tissue. This zone gradually merges into a posterior region, which still possesses large Malpighian corpuscles and distinct secretory tubules.

In the two oldest males (*H.L.* 18 and 20 mm.), the epididymis is well developed. It lies dorso-laterally to the testis in a large cavity close to the ventral side of the abdomen, just cranially to the scrotal sac, and consists of many canals, which join together into a single rete duct with darkly staining walls. This duct, which is somewhat smaller than in Dasyurus, Stage K, runs ventro-medially through the mesorchium, to be connected with the seminiferous tubules. No paradidymis appeared to be present. In the female of the same age (*H.L.* 18 mm.), a similar duct passes from the centre of the ovary through the mesovarium, but its opposite end was not traced, owing to this portion being absent from the sections. Most probably the duct is a blind tube as in the female of other forms.

In *Metachirus* (*H.L.* 13 mm.), the conditions are much as in Didelphys. On the left side, only three tubes appeared to pass from the rete duct into the epididymis, but, on the right, it was difficult to count the exact number.

The urogenital connection in Didelphys is therefore made up of a single rete canal, which becomes connected with 11 or 12 mesonephric tubules, the latter developing into the epididymis (text-fig. 8, *B*).

Perameles. In an embryo of Perameles with a length of 6·8 mm., the cranial portion of the excretory organ, which begins on a level with the 4th spinal ganglion, consists of many rudimentary tubules, the majority of which have a solid nephrostomial connection with the coelomic epithelium. Behind

the level of the 6th spinal ganglion, the tubules are larger, and definite primordia of Malpighian corpuscles are present. Further posteriorly, they become curved, and much resemble the developing mesonephric tubules in the Trichosurus embryo of 4·5 mm. *G.L.* (Stage II) (cf. Part I of this paper). The wall of that portion of each of these posterior tubules, which is destined to develop into a Malpighian corpuscle, is connected with the coelomic epithelium on the ventro-medial side of the urogenital fold by what must be regarded as a rudimentary nephrostomial canal. These structures (Pl. IX, figs. 7 *a*, *b*, and 8 and Pl. VIII, fig. 7, *nph.*) are present all along the excretory organ, right down to the posterior end, where additional tubules are still forming. The majority of them take the form of a thick column of denser cells, whose margins are not definitely limited from the surrounding mesenchyme (Pl. IX, fig. 8, *nph.*). Some of the columns are narrower and not so well developed, whilst a few are longer and partly tubular (Pl. VIII, fig. 7, *v.nph.*), and in some cases a slight groove in the coelom is present opposite the point of contact with the coelomic epithelium. It is noteworthy, also, that in some instances they tend to run into each other.

The suprarenal primordium stretches from the level of the 5th to behind the level of the 12th spinal ganglion. Its cranial end is poorly developed, but further back it is well marked, and is seen as a continuous proliferation of cells from the coelomic epithelium, which passes up dorsally between the aorta and the mesonephros. Along its posterior region it is connected with the rudimentary mesonephric nephrostomes at this level by bands of cells, which extend out dorso-medially from each nephrostome to blend with the cells of the primordium (Pl. IX, fig. 7, *a*, *b* and *c*). These outgrowths from the nephrostomes apparently contribute towards the formation of the cortical substance of the suprarenal body.

The genital ridge is not yet developed.

In the next embryo of Perameles (*G.L.* 7 mm.) and in later stages, the genital ridge is present as a low elevation filled with denser cells, extending along the ventro-medial side of the urogenital fold, and quite similar to that in the early stages of Trichosurus and other forms. The cells within the anterior portion of the ridge, which eventually form the rete core, lie in exactly the same place as the degenerate nephrostomial canals present in the embryo of 6·8 mm., and they approach close to the walls of the Malpighian corpuscles. In the 6·8 mm. embryo, the cells of those nephrostomial canals, which are not definitely separated from the surrounding mesenchyme (Pl. IX, fig. 8, *nph.*), have a similar appearance to the cells in the genital ridge of the next stage (*G.L.* 7 mm.). The evidence points to the conclusion that the rete core is derived from the nephrostomial canals and nephrostomes.

In a female with a head length of 12·5 mm., the rete is becoming transformed into a single hollow tube, which is connected by a few solid cords with Malpighian corpuscles in the anterior part of the mesonephros. The cranial end of the tube could not be definitely followed, but it eventually runs into

the anterior end of the Wolffian duct. In an older female (*H.L.* 16 mm.) there is a definite rete duct, the cranial end of which was again rather indistinct. On the left side, it appears to be connected with the Wolffian duct by several tubules, which no longer possess glomeruli; the condition on the right is apparently somewhat similar. The cranial end of the mesonephros is now very degenerate, but in the posterior portion glomeruli are still present. In a still older stage (*H.L.* 37 mm. ♀), the rete duct runs out from the centre of the ovary through the mesovarium. It then becomes narrower and passes into the epoophoron, now devoid of tubules and almost completely atrophied, and, coiling round, it terminates in a degenerating cord, which evidently represents the last vestige of the anterior end of the Wolffian duct. In older females, the rete duct does not reach beyond the mesovarium.

In a male with a head length of 19 mm., the epididymis is composed of a small number of short tubules, about four or five, forming a network lying in connective tissue on the dorsal side of the testis. From the conditions in the younger female (*H.L.* 12·5 mm.), it is very possible that these canals represent a similar number of modified mesonephric tubules.

The urogenital connection in Perameles would thus seem to involve a single rete canal and a small number (presumably 4 or 5) of mesonephric tubules from which the epididymis arises (text-fig. 8, *C.*).

DIPROTODONTIA

Phascolarctos. Observations on a series of embryos and pouch young of Phascolarctos (*G.L.* 7·5, 9, 11, 12·25, 13·5, 16·5 mm., *H.L.* 9 and 9·5 mm.) show that the development of the rete is apparently identical with that of Trichosurus. A similar rete ridge is present in early stages, and in later pouch young (*H.L.* 9·5 mm.), all of which are female, the rete is composed of a mass of cords, some of which are tubular. They pass from the centre of the ovary through the mesovarium, and are united by solid cords of cells with the walls of the Malpighian corpuscles. Further anteriorly, the rete forms a single cord, which runs forwards close up to the medial side of Bowman's capsules, and, as in other forms, it is seen to be connected with the coelomic epithelium of the ridge.

In the oldest stage of Phascolomys (*G.L.* 17·5 mm. ♂) which was investigated, the rete ridge was well defined, but a rete cord had not yet developed.

Several female Macropods (*M. thetides*, *H.L.* 22 mm., *M. ruficollis*, *H.L.* 23 and 32 mm., and *Petrogale pencillata*, *H.L.* 7·5 to 8 mm.) were also examined. In all these there was a well marked broad rete, consisting of many small tubules, some larger than others, extending out from the central mass of the ovary through the mesovarium to run into the epoophoron. The latter was made up of narrow canals, representing the remains of the anterior end of the mesonephros. The condition in the oldest female recalls the description and figures given by van den Broek ('05) of the rete ovarii of an adult Petrogale.

SUMMARY

Diprotodontia. The number of stages of genera older than Trichosurus, available for study, unfortunately does not form a complete series, but the results so far obtained seem to show that in this suborder the conditions described for Trichosurus generally hold good. The rete core becomes attached to a considerable number of Malpighian corpuscles (17 or 18 in Trichosurus) at the anterior end of the mesonephros. The rete eventually divides into a large number of fine canals, which run out from the gonad through the mesogenitale into the epididymis or epoophoron. The epididymis arises from the anterior mesonephric tubules, by transformation of their secretory portions and of their Malpighian corpuscles, as described in Trichosurus (text-fig. 8, *A*).

Polyprotodontia. In all the Polyprotodonts so far investigated, the rete core, instead of breaking up into many fine canals, develops into a single large duct.

In Didelphys, as in Trichosurus, the anterior end of the rete core lies close against the walls of the most anterior Malpighian corpuscles, whilst, more posteriorly, a connection with the latter is established by means of sprouts from the rete itself. During this process, the rete core develops into a single rete duct, which stretches from the anterior end of the mesonephros through the mesogenitale into the gonad. The epididymis arises from a fairly large number of anterior mesonephric tubules (possibly 11 or 12), which become transformed into uniformly narrow canals as in the Diprotodontia (text-fig. 8, *B*).

In Perameles, a single rete duct is again developed, but apparently only a very limited number (possibly 4 or 5) of the anterior tubules of the mesonephros take a share in the formation of the epididymis, the rest of the excretory organ completely degenerating (text-fig. 8, *C*).

In Dasyurus, there appears to be a temporary attachment between the rete duct and a number of Malpighian corpuscles at the anterior end of the mesonephros. Eventually, however, the duct only remains united by a single canal, probably the first mesonephric tubule, or the first and second fused together, with the Wolffian duct (text-fig. 8, *D*). The mesonephros completely degenerates into a mass of connective tissue, in which the single duct undergoes a complicated coiling to form the epididymis. Van den Broek ('06) has already put forward the suggestion that the tube passing from the Wolffian duct into the genital gland of Dasyurus and Sminthopsis might possibly represent the most cranial tubule of the mesonephros, which grows into the gonad, though he thought this suggestion unlikely. This author did not observe any transformation of mesonephric tubules into a connecting duct, and he was not in a position to make any investigations on the development of the rete, such as has been described in this paper.

DISCUSSION

There is much difference of opinion as regards the origin of the rete cords in the Amniota. Many of the earlier workers, such as Braun ('77), Weldon ('85), and Hoffmann ('89) in reptiles, Hoffmann ('86) in Amphibia, Schmiegelow ('82) and Semon ('87) in the chick, Mihalkovics ('85) in the cat, dog, and rabbit, and more recently Sainmont ('06 and '08) in the cat, and von Winiwarter ('08, '00 and '10) in the rabbit and man, consider that the rete develops entirely from outgrowths of the walls of a variable number of Malpighian corpuscles at the anterior end of the mesonephros. According to this view, the rete does not appear until shortly before the involution of the mesonephros.

A second opinion, held by Janosik ('85), and later by Coert ('98) in his investigations on the rabbit and cat, and Allen ('04) in his studies on the pig and also on the rabbit, ascribes the origin of the rete cords to invaginations of the peritoneal epithelium. Coert ('98)[1] thinks that the rete tubules develop from a mass of cells lying within the genital ridge, the so-called "Reteblasteem," which is derived from cells of the coelomic epithelium, which slowly migrate inwards. Allen ('04) describes the primordium of the rete in the pig as tubular invaginations of the peritoneum, which are formed at the same time and in the same manner as the sex cords (both medullary cords and seminiferous tubules). The union with the Malpighian corpuscles is therefore a secondary one.

A few of the more recent authors, namely Bouin ('00) in the frog, Wichmann ('12) in the sheep and dog, and Firket ('14) and Swift ('15) in birds, contend that the urogenital connection is derived from the mesenchyme lying between the peritoneal epithelium and the Malpighian corpuscles. Here again, the rete is regarded as becoming only secondarily connected with the uriniferous tubules. Wichmann and Firket consider that the urogenital cords are homologous with pronephric nephrostomes, which have lost their connection with the coelomic epithelium. In Chrysemys Allen ('05) states that the rete arises from a series of "funnel-cords" which take their origin from peritoneal funnels of the Malpighian corpuscles. In this last paper, the divergent views on the development of the rete are well shown in a series of diagrams.

In the early stages of Trichosurus I was not able to trace the exact origin of the cells which come to lie within the rete ridge, but appearances in this genus at first suggested that a gradual infiltration of cells from the coelomic epithelium was taking place during this time, such as is said to occur in the rabbit according to Coert ('98). With the exception of Perameles, the conditions in the early stages of other marsupials much resembled Trichosurus. The youngest embryo (*G.L.* 6·8 mm.) of Perameles is of special interest. In this stage, immediately behind what may be regarded as the region of the pronephros, the portions of the tubules destined to become the Malpighian

[1] My knowledge of Coert's paper was obtained from the references in the papers of von Winiwarter ('10), Allen ('04) and Wichmann ('12). I have had no opportunity of reading the original.

corpuscles are connected with the coelomic epithelium by a series of rudimentary nephrostomial canals, which are found as far back as the posterior end of the excretory organ, where tubules are still forming. The majority of these nephrostomial canals have the form of rather thick, cellular columns, of somewhat indefinite outline, owing to the fact that their margins are not sharply marked off from the surrounding mesenchyme. Moreover, adjacent canals tend to run into each other. In a slightly older embryo (*G.L.* 7 mm.), mesonephric nephrostomes are no longer recognisable, but between the Malpighian corpuscles and the coelomic epithelium we find a continuous mass of denser cells lying in a low ridge, which projects into the coelom along the ventro-medial border of the urogenital fold. This ridge is the primordium of the genital ridge, and is exactly similar to that present in early stages of Trichosurus and other forms. The comparison of these two embryos of Perameles leads to the conclusion that in this genus, and probably also in Trichosurus and other marsupials, the cells within the genital ridge are derived from the nephrostomial canals of the mesonephros, which lose their connection both with the coelomic epithelium and the Malpighian corpuscles, and unite into a continuous mass of cells.

The exact determination of the origin of the cells in the genital ridge in early stages in other forms is evidently a matter of some difficulty. This is noted in the chick by Firket ('14), who says (p. 218): " Il n'est pas facile de distinguer, lors les premiers stades du développement des glandes génitales, ce qui est tissue mésenchymatique de ce qui est épithélial." Coert ('98) experienced the same difficulty in the rabbit, whilst Allen ('04) finds the peritoneal invaginations much clearer in the pig than in the rabbit. Wichmann ('12), also, refers to the fact that the elements are more easy to distinguish in some animals than in others. In the sheep, dog, and pig, he describes bridges of cells stretching from Bowman's capsules to the coelomic epithelium. These bridges much resemble the rudimentary mesonephric nephrostomes present in Perameles. According to this author, the cell bridges, lying near the cranial part of the genital primordium, early run into each other, and thus form a continuous blastema, which is indistinctly separated from the surrounding mesenchyme. Out of this blastema the rete later differentiates. This description of the origin of the rete blastema coincides very closely with the conditions described in Perameles. Wichmann, however, considers that in the forms investigated by him, the cell bridges are derived from the primary nephrostome canals ("Ergänzungskanälchen") of the pronephros. This is certainly not the case for Perameles, nor for other marsupials, where the anterior end of the rete ridge always lies behind the region of the pronephros. In coming to this conclusion, Wichmann necessarily assumes that pro- and mesonephric elements are present in the same segments of the body, but, as already stated in Part I of this paper, there is no evidence of such overlapping in marsupials.

Allen ('05), as already noted, also ascribes the origin of the rete in Chry-

semys to the peritoneal funnels of the Malpighian corpuscles, which become detached from the latter and develop into "funnel-cords." In later stages, these unite with short evaginations from Bowman's capsules, and thus establish the urogenital connection. Such short outgrowths from the walls of the Malpighian corpuscles were also observed in Trichosurus, but, as in Chrysemys, they are of small importance, and certainly take a very insignificant part in the formation of the rete. Again, in Elasmobranchs, according to Borcea ('05), the vasa efferentia[1] take their origin from a variable number of nephrostomial canals.

In Stages V and VI of Trichosurus, the anterior end of the genital ridge is continuous with the hinder end of the suprarenal primordium. This connection has been observed and variously interpreted by different authors. Soulié ('03), who has made extensive studies on the development of the suprarenal bodies in higher vertebrates, considers that the apparently perfect fusion between the two organs is a result of their common origin from the coelomic epithelium, and is thus of only secondary significance. The suprarenal primordium in Trichosurus is certainly well marked before the genital ridge first definitely appears. In the embryo of Perameles with a length of 6·8 mm. the nephrostomes towards the cranial end of the mesonephros are connected by bands of cells with the hinder end of the suprarenal primordium (Pl. IX, fig. 7 *c*, *x*). These structures appear to be almost exactly similar to the "funnel-cords" of Chrysemys; according to Allen, the "funnel-cords" extend dorso-medially from the peritoneal funnels, their proximal ends forming the major part of the rete, whilst their distal ends fuse with the primordium of the suprarenal body, and, in his view, contribute the greater part of the cortical substance of this organ, only a small portion being furnished by peritoneal ingrowths. The connection between the nephrostomes and the suprarenal organ in Perameles is of short duration, and, although they apparently take some part in the development of the latter, the extensive proliferations from the coelomic epithelium, directly medial to the nephrostomes, evidently form the main source from which the suprarenal cortex arises. The nephrostomes opposite the hinder portion of the suprarenal primordium seem to disappear completely, together with their mesonephric canals, only those behind this region developing into the rete. In Trichosurus, the connection between the anterior end of the genital ridge and the suprarenal organ very soon disappears, and a short time after the ostium abdominale is developed, the cranial end of the ridge runs directly into the epithelium of the shallow medial bay of the ostium. The meaning of this relation is obscure, but there is no direct evidence that the ostium abdominale has anything to

[1] It must be noted that, in Elasmobranchs, according to Borcea, the vasa efferentia only represent the transverse tubules, which lead from the collecting canal of the testis to the longitudinal canal of the epididymis, the connections between the latter and the Malpighian corpuscles being termed "canalicules intermédiaires." This distinction is not possible in the Mammalia, and the term rete or vasa efferentia, adopted in this paper, refers to the whole length of the canal or canals, which unite the seminiferous tubules with the Malpighian corpuscles.

do with pronephric nephrostomes and canals (cf. Part I of this paper), as supposed by Wichmann ('12, '14), when he discusses the presence of connections in the pig and in man, during the beginning of the foetal period and sometimes later, between the epithelium of Müller's duct and the tubes of the rete ovarii and epoophoron.

The rete ridge in Perameles, in embryos older than 6·8 mm., and in early stages of other marsupials, is the direct continuation of the genital ridge and is apparently identical with the latter, exactly as described by Allen ('04) in the pig. The two are indistinguishable, and the differentiation into gonad and rete does not occur until shortly before birth. At this time and in later stages, after the rete core is established, definite cord-like invaginations are seen uniting the coelomic epithelium of the ridge with the rete core. They have the same appearance as the sex cords, which are now developing in the gonad. Allen ('04) considers that the rete cords of the pig are formed from tubular invaginations of the peritoneum, which arise at the same time and in the same manner as the sex cords. When comparing the results of his investigations on Chrysemys and mammals, he finds it difficult to be certain of the nature of the rete in the latter, and suggests (p. 93) that either "the sex-cords have disappeared leaving only the funnel-cords," or, more probably, "the sex-cords which presumably existed in this region have taken on the function and character of funnel-cords." I have had much the same difficulty in interpreting the significance of the definite ingrowths of the coelomic epithelium, which occur in later stages of Trichosurus, Didelphys and other forms, but am inclined to agree with Allen that they represent sex cords. It might be supposed that they are homologous with the sex cords of the definitive gonad, a relic of the time when the latter extended further cranially. The fact that they come into close relation with the rete core suggests that they may take a part in the later development of the rete, but whether this is so or not, I have not been able to determine. It is not impossible that in some of the higher mammals, such as the pig, the sex cords, as suggested by Allen, may alone form the urogenital connection, completely replacing the nephrostomes.

The transformation of the rete core into a single duct in the Polyprotodontia recalls the longitudinal canal, which is developed in many of the lower Vertebrates. In most Elasmobranchs, the nephrostomial canals which form the vasa efferentia, terminate in rudimentary vesicles, which unite to form the so-called longitudinal canal of the epididymis (Borcea, '05), the latter entering into relation with the Malpighian corpuscles of the mesonephros by means of a number of intermediate canals corresponding to the number of nephrostomes. A similar longitudinal canal ("Nierenrandkanal") is present in Amphibia and also in some reptiles, such as the viper. In Amphibia, according to Hoffmann ('86), the vasa efferentia are formed by means of sprouts, which grow out from the Malpighian bodies through the mesogenitale into the gonad. Before the sex is differentiated, other sprouts arise from the

part of the vasa efferentia lying nearest to the kidney, and these unite into a canal ("Längskanal") running along the medial edge of the latter. Semon ('92) considers that this system of cross and longitudinal canals in Amphibia takes its origin from the segmental strands, which represent the inner portions of the primitive connection between the nephrostomes and the coelom. Again, in the viper (Braun, '77), the longitudinal canal is said to be produced by the union of outgrowths, which spring from the Malpighian bodies of that part of the mesonephros situated near to the gonad. In many reptiles, the longitudinal canal is incomplete, as in the turtle (Allen), or is in the form of a long often broken cell strand, as in the lizard and slowworm (Braun). The single rete duct, which, in certain early marsupial pouch young, resembles the longitudinal canal in reptiles and Elasmobranchs, becomes shortened in later stages, owing to the shrinkage of the anterior end of the mesonephros and to the form of the testis. It finally comes to consist of a short tube, leading from the seminiferous tubules through the mesorchium into the epididymis.

The involution of the mesonephros to form the epididymis and paradidymis in the male, and the epoophoron and paroophoron in the female, follows in many particulars the course of events in the cat as determined by von Winiwarter and Sainmont ('08). The transformation of the mesonephric tubules and of the Malpighian corpuscles appears to take place in the same manner as observed by these authors. In the higher Mammalia, a large number of these tubules apparently take part in the formation of the epididymis. In the Marsupialia, however, the number varies considerably in different genera, being 17 or 18 in Trichosurus, 11 or 12 in Didelphys, 3 or 4 in Perameles, and only one (or possibly two) in Dasyurus. A similar variation is found in the Reptilia, and again in Elasmobranchs. Amongst the latter, the epididymis[1] in Squatina is formed from six of the anterior mesonephric canals, which unite with a corresponding number of vasa efferentia, in Mustelus and Galeus there are three to five, whilst in the rays there is only one vas efferens, which becomes connected with the Wolffian duct by means of the first incompletely formed mesonephric tubule. The exact mode of origin of the epididymis in reptiles needs further investigation. In this order, it is usual for a number of the connections between the vasa efferentia and the Malpighian corpuscles to be absorbed during early life. In the lizard and in snakes (Braun, '77, Hoffmann, '89) many such connections are developed, but they all degenerate with the exception of two or three, which form the ducts leading from the testis into the epididymis in the adult. In adult Chelonians, although the number of canals uniting the testis with the epididymis is a larger one than in lizards or snakes, here also there is a considerable reduction during the process of development. For example, in a young *Emys lutaria*, measuring 2·5 cm., there are, according to von Möller ('99),

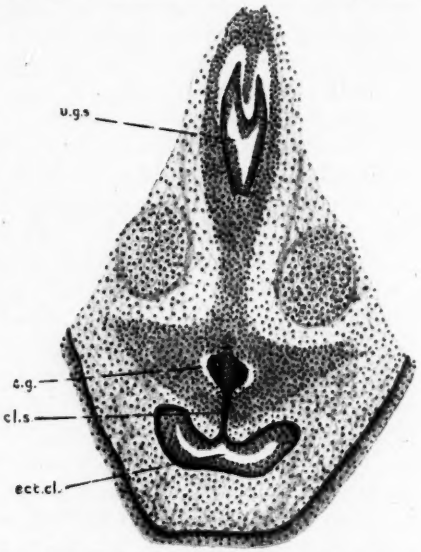
[1] The epididymis in Elasmobranchs, as defined by Borcea ('05), is that part of Leydig's gland which is in connection with the vasa efferentia.

about 30 rete cords, whilst in the adult this number is reduced to 15. Again in Chrysemys (Allen, '05), the rete cords amount to 16 in an embryo of 8 mm., whereas in the fullgrown turtle only 9 were counted. It will be remembered that in Dasyurus (Stages I and J) there is also an abortive attempt on the part of the rete to become attached to several of the tubules at the anterior end of the mesonephros. In snakes, the epididymis is much less developed than in other reptiles, and simply consists of a coiled portion of the vas deferens, which communicates by two or three canals with the testis. This condition presents a striking parallel with the mode of development of the epididymis in Dasyurus. It is of interest to note that the canals of the epididymis in Echidna (Disselhorst, '97) are also few in number, and separated by much connective tissue, but how these canals arise has not yet been investigated.

ACCESSORY GLANDS

Cowper's Glands. Well developed Cowper's glands are present in the male Trichosurus. They are also developed in the female, but always remain small and probably undergo reduction in older pouch young.

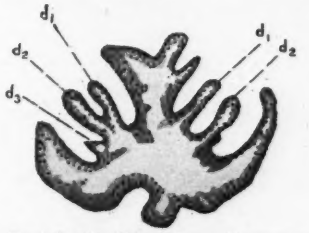
The primordia of the glands first appear in a male foetus with a length of 16 mm. (*H.L.* 6·5 mm.) in the form of two slight solid outgrowths from the ventro-lateral wall of the urogenital sinus (text-fig. 9, *c.g.*), just at the point where the free margin of the cloacal septum reaches the latter. In pouch young with a head length of 7·5 mm., both male and female, these outgrowths have developed into definite short buds, extending out from the sinus wall (Part I, text-fig. 14, *c.g.*). They grow rapidly and very soon (*H.L.* 8·5 mm.) stretch up dorsally on each side of the sinus, ventro-laterally to the rectum. In succeeding stages, the primordia, originally single and solid, become hollowed out and branched, and the resulting glands in the male soon attain a larger size than those of the female. In Part I of this paper, text-fig. 25 (*l.c.g.*, *r.c.g.*) shows a transverse section of Cowper's glands in a



Text-fig. 9. *G.L.* 15 mm. *H.L.* 6·75 mm. Transverse section, showing the primordia of Cowper's glands (*c.g.*), arising from the ventro-lateral wall of the urogenital sinus. The free margin of the cloacal septum (*cl.s.*) meets the urogenital sinus in the sections immediately following. *cl.s.* dorsal margin of cloacal septum, forming ventral wall of urogenital sinus; *ect.cl.* ectodermal cloaca; *u.g.s.* urogenital sinus. (Sl. 6–5–5.)

male with a head length of 11 mm., whilst the point of origin of the glands from the urogenital sinus in older stages is shown in Part I, text-figs. 15, 18, 19, 21 and 23 (*c.g.*). With the general growth of the sinus wall, the glands gradually come to open on the dorsal side of the latter (text-fig. 10).

In the male with a head length of 26 mm., each gland arises from the sinus by two short hollow ducts, which lie close together. Running up dorsally, they spread out into numerous glandular lobes, which reach up on each side of the rectum. A third duct is now present on each side, arising from the sinus posterior to and quite separate from the first two, but though hollow, it is only a short sprout. In older males, these ducts apparently tend to unite into one common opening, and their number appears to vary slightly. For example, in a foetus with a head length of 3·1 cm. we find the glands leading into the sinus by one dorsal duct, which branches almost directly into two, and by one smaller ventral duct, on each side. Again, in a slightly older specimen (*H.L.* 3·5 cm.), there are four narrow ducts, one of which is very small; the largest appears to be independent, but the other three join together almost immediately into a common tube. In the oldest male foetus (*H.L.* 4·1 cm.), three ducts are again found, lying close together, two of which (text-fig. 10, *d* 1. *d* 2) unite almost at once on leaving the sinus. At this stage, as may be seen from the text-figure, the urogenital sinus at the level of Cowper's glands, has a three-cornered shape in cross section, the dorso-lateral walls, into which the glands open, being convex towards the cavity of the sinus. The usual number of ducts appears to be three, and these most probably correspond to the three pairs of Cowper's glands generally present in Marsupials (van den Broek, '10 *a*). In most cases, van den Broek ('10 *a*) finds that one pair is very small, whilst the other two lie so close together that they are difficult to separate from each other. Possibly in Trichosurus, the two anterior ducts originate by secondary division from the primitively single outgrowth, which first appears in pouch young with a head length of 6·5 mm.



Text-fig. 10. *H.L.* 4·1 cm. Transverse section of the urogenital sinus at the level of the openings of Cowper's glands (*d* 1, *d* 2, *d* 3). (Sl. 9–1–5.)

In an adult male, dissected by Mr K. S. Tan, there were two pairs of Cowper's glands, one pair being considerably larger than the other.

In a female with a head length of 38 mm., the glands are not nearly so large, being shorter and less branched than in the male of 26 mm. *H.L.* They spring from an apparently solid duct on each side, which divides into several small hollow lobes. These stretch up on each side of the urogenital sinus, but do not extend above the latter, not reaching nearly so far dorsally as in the male. In the oldest female (*H.L.* 4·6 cm.), they have not increased in size and are perhaps even less well developed.

From our account of the origin of the cloacal septum from the coalesced walls of the entodermal cloaca, it is evident that Cowper's glands, arising as they do from the ventro-lateral walls of the sinus just where the free margin of the septum runs into the wall of the latter, must be of entodermal origin. This is easily realised by a glance at text-figs. 14 and 15 (*c.g.*) in Part I of this paper. From the situation of the glands in older pouch young, van den Broek ('07 and '10 *a* and *b*) supposes that they develop from the oral wall of the entodermal cloaca, and regards them as marking the limit between ectoderm and entoderm. Their apparent position between ectoderm and entoderm is due to the fact that, in older stages, the epithelium of the urogenital sinus, from the opening of the latter as far forwards as Cowper's glands, secondarily takes on an epidermal appearance, as pointed out in Part I of this paper (section on Cloaca). In any case, however, the question of the origin of Cowper's glands is closely bound up with the mode of development of the cloacal septum, which has received various interpretations by different authors (Part I, p. 69).

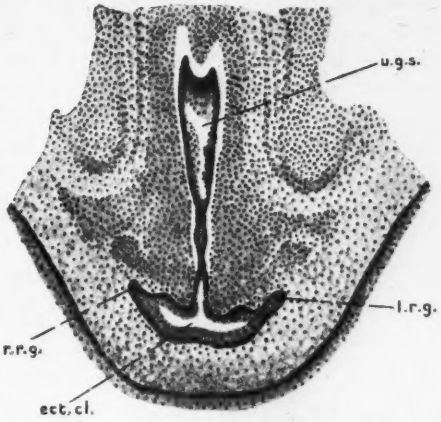
Urethral Glands. Urethral glands are developed in the male, but they were not observed in the female. The primordia of the glands were first seen in a male pouch young with a head length of 20 mm. (*G.L.* 4 cm.). At this stage, they appear as short, solid, bud-like outgrowths, which arise from all round the wall of the urogenital sinus, from the entrance of the Wolffian ducts to about half way along the length of the sinus, gradually becoming less marked towards their posterior limit. In a male with a head length of 26 mm. they are better developed, being largest near the entrance of the Wolffian duct, where they branch out into many short solid lobes. They decrease in size posteriorly, and no primordia are apparent beyond the anterior two-thirds of the sinus. These observations on the urethral glands agree with those of van den Broek ('07, '10 *a*), who also finds the primordia appearing late in development, i.e. Dasyurus, *D.C.L.* 53 mm.

In the adult they form a conspicuous glandular swelling round the urethra, the so-called "prostate" gland. The swelling is thickest near the neck of the bladder, and gradually tapers towards the posterior end, which lies some distance in front of the openings of Cowper's glands.

Cloacal Glands. Cloacal or so-called rectal glands are well developed in both sexes. There is one large dorsal pair of glands and a variable number of smaller subsidiary pairs.

They first appear in the newly born foetus (*G.L.* 14·5 to 15 mm.), in the form of a slight outbulging of the lateral wall of the ectodermal cloaca on each side, close to the entrance of the rectum into the latter. They therefore develop at a slightly earlier stage than do Cowper's glands. In pouch young with head lengths of 6·5 to 7·5 mm. (*G.L.* 15 to 17·5 mm.) they are more conspicuous, now forming short solid outgrowths (text-fig. 11, *l.r.g.*, *r.r.g.*). During the next stages, the primordium increases in length and develops into a short hollow duct, the distal solid end of which is enlarged, and is

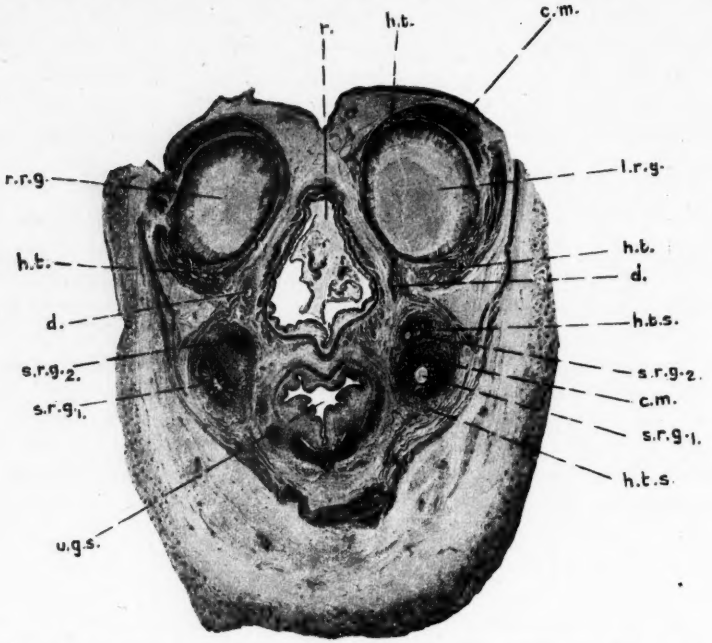
surrounded by a condensed mass of mesenchyme. The duct grows gradually longer, and, in pouch young with head lengths of 11 to 12 mm., extends up dorso-laterally, swelling out at its distal end into a large, almost solid, bulbous enlargement, situated dorso-laterally to the posterior end of the rectum. The distal enlargement, which represents the primordium of the gland proper, consists at first of a small central area of lighter cells with faintly staining nuclei, surrounded by a wider darker layer of epithelial cells. Very soon (*H.L.* 12·5 mm.) a central cavity appears, in which lie clumps of degenerating, pale staining cells, whilst the outer investing layer of epithelium becomes much thinner. The duct, immediately after leaving the gland, branches into several short hollow tubes, which, at this stage, extend round the ventral half of the gland. Meanwhile, from the lateral walls of the cloaca on each side, three more solid outgrowths have arisen close to the primary duct, two lying ventrally, and one dorsally to the latter. These are eventually destined to develop into smaller subsidiary glands, which are situated ventrally and posteriorly to the large pair. Their first development is very similar to that of the latter, but their central cavity always remains small, their distal ends early dividing up into many small lobes. They are already well marked in a foetus with a head length of 26 mm., where we find three subsidiary glands on the left side and two on the right; in the most ventral one of each side a central cavity is beginning to form, whilst the others are as yet quite solid. In a much older male (*H.L.* 4·1 cm.) there are still only two pairs of very small subsidiary glands. They are deeply lobed, possess a well marked cavity, and are surrounded by a ring of narrow tubules. Their ducts communicate with the cloaca, one just dorsally, the other shortly ventrally to the duct of the main cloacal gland.



Text-fig. 11. *G.L.* 15 mm. *H.L.* 6·75 mm. Transverse section, showing the origin of the cloacal glands (*r.r.g.*, *l.r.g.*) from the lateral wall of the ectodermal cloaca (*ect.cl.*). *u.g.s.* urogenital sinus. (Sl. 6–5–11.)

The oldest foetus, in which the cloacal glands were examined, was a female with a head length of 4·6 cm. Here, we find a large dorsal anterior pair of glands (text-fig. 12, *l.r.g.*, *r.r.g.*), lying dorso-laterally to the rectum on each side. Each has an average diameter of about 2·5 mm. The very large central cavity is encircled by an inner wall of a few layers of pale staining cells, around which is a very thin outer investment of small darkly staining cells. The edge of the gland is indented to form small lobes, and around it is a well

marked circular layer of striate muscle (*c.m.*). The duct (*d.*) is a long narrow tube, which extends back on each side of the rectum to open finally into the lateral side of the cloaca. From the duct, near its entrance into the gland, arise numerous hollow tubules (*h.t.*), which run all round the gland, but are especially abundant on the ventral side. Ventral and posterior to the large cloacal gland are four small glands, lying close together on each side. Of these, the two most anterior (*s.r.g.l.*) are the largest, but, nevertheless, they are



Text-fig. 12. *H.L.* 4·6 cm. ♀ Microphotograph of a transverse section, showing the posterior portion of the large dorsal cloacal glands (*r.r.g.*, *l.r.g.*), and the most anterior pair (*s.r.g.* 1) of subsidiary glands. The anterior end of the second pair of subsidiary glands (*s.r.g.* 2) is also seen, just beginning to appear dorsally to the first pair. *c.m.* circular layer of muscles; *d.* duct of large cloacal gland; *h.t.* narrow tubules surrounding large gland; *h.t.s.* narrow tubules round subsidiary glands; *r.* rectum; *u.g.s.* urogenital sinus. (Sl. 8–3–7. × 10.)

very considerably smaller than the main gland. They are surrounded, like the latter, by hollow tubules (*h.t.s.*) and by a circular layer of muscle fibres (*c.m.*); they are lobulated, and contain a well marked cavity. The most ventral of the subsidiary glands on the right side is very small and poorly developed. Their ducts, which are long and narrow, open two dorsally, and two ventrally to the duct of the large gland.

In the adult male, dissected by Mr K. S. Tan, there were two pairs of arge cloacal glands, the more dorsal anterior pair communicating with the

cloaca by a long narrow duct on each side, whilst the ducts of the more ventral and slightly larger pair were very short.

According to van den Broek ('04), there are usually in adult marsupials only two pairs of cloacal glands, of which the more ventral one is often much better developed than the more dorsal. In 1836, Martin ('36) mentions the occurrence of four rectal glands in *Trichosurus vulpina*, and later, in 1882, Cunningham ('82) figures and describes in *Trichosurus maculata* three pairs of glands, two near the anus, and one pair situated more orally at the side of the rectum, each gland having an independent duct. In the vulpine phalanger, according to this author, the same number of glands were present, but they were smaller in size. Very possibly the number of glands may vary even in the same species. Whether the four subsidiary pairs in the foetus with a head length of 4·6 cm. always remain small, one or two pairs being quite rudimentary, or whether some of them develop later into definite cloacal glands, I have not determined.

Other accessory glands. In the later stages of pouch young, surrounding the dorsal and to a less extent the ventral side of the cloaca, there are small tubules, which are exactly similar to those round the cloacal glands above described. They are united with the wall of the cloaca by many fine ducts, and evidently arise independently as outgrowths from the cloacal wall. It may be noted that, of these tubules, the more lateral ones appear to be in connection with those around the most dorsal of the subsidiary cloacal glands on each side. These tubular structures apparently correspond to the branching tubular glands ("verzweigte tubulöse Drüsen") described by van den Broek ('07, p. 380) in the neighbourhood of the cloaca, their exact significance being doubtful.

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REFERENCE LETTERS

gl. glomerulus; *r.c.* rete core; *r.r.* rete ridge; *v.c.* vena cava; *W.D.* Wolffian duct; *L.* lateral; *M.* medial.

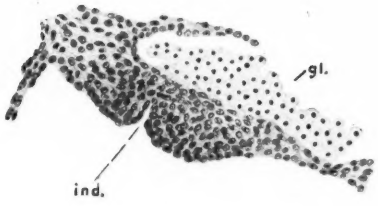
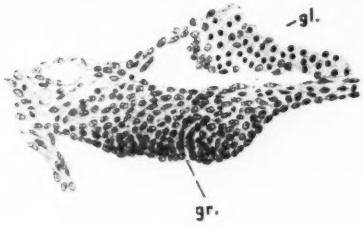


FIG. 1



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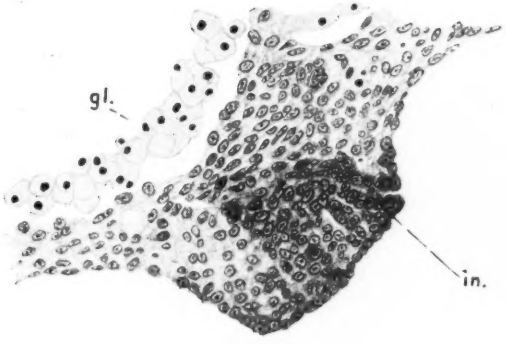

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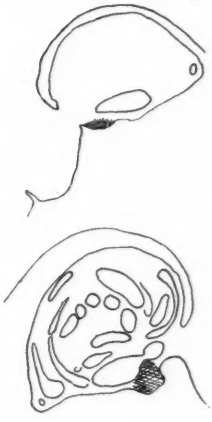

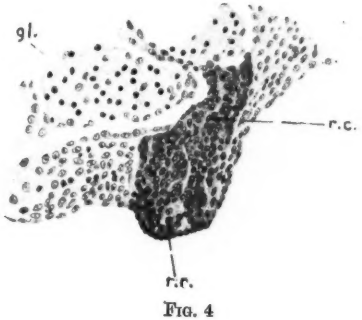

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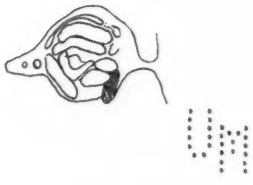

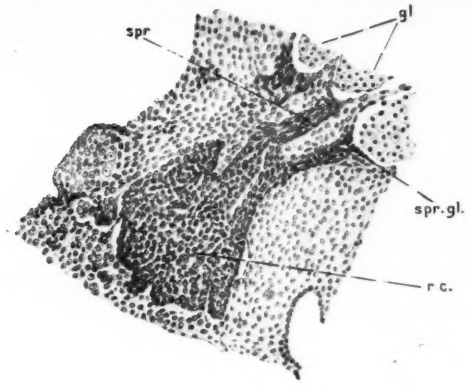

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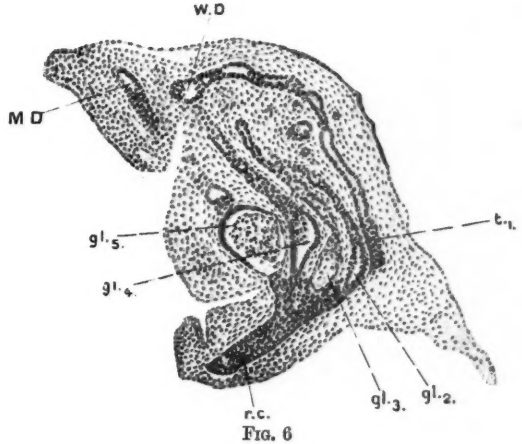

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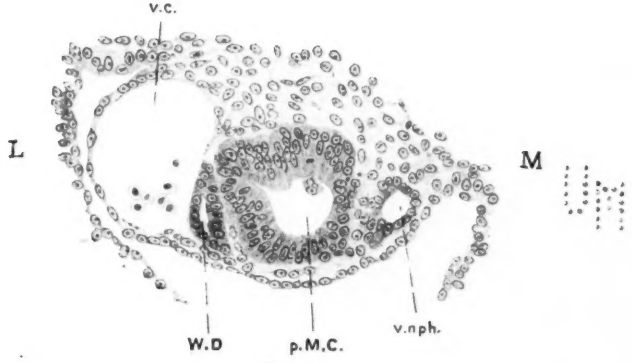

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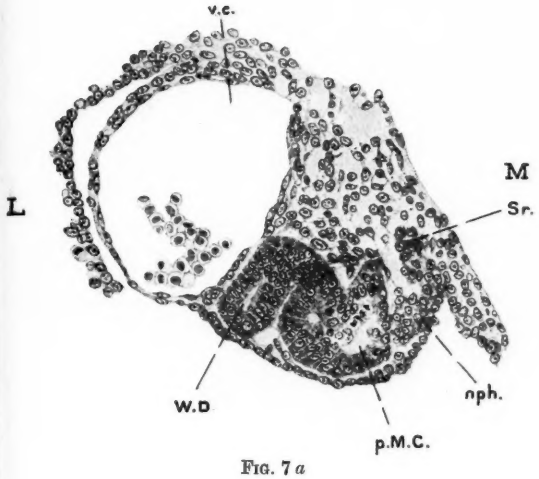
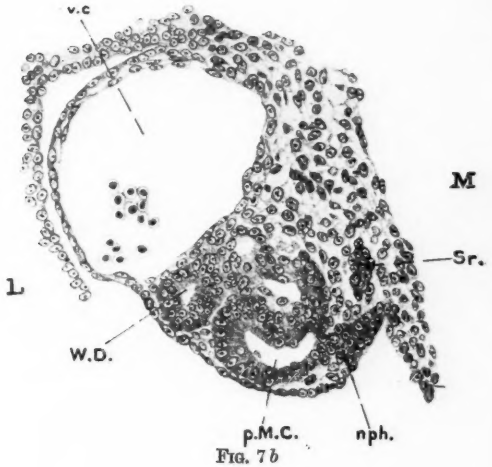


FIG. 7 *a*



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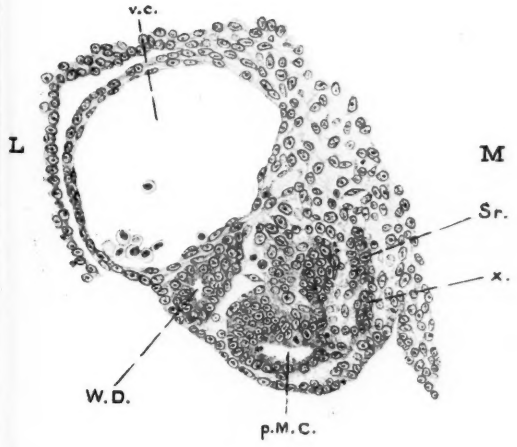

FIG. 7 *c*

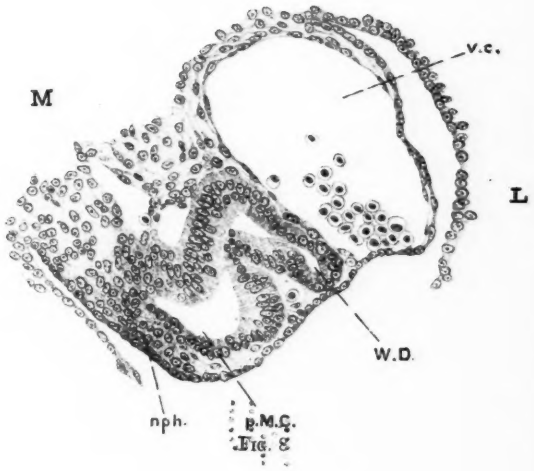

FIG. 8

DESCRIPTION OF PLATES

Fig. 1. *Trichosurus vulpecula*, Stage XII, *G.L.* 11·5 mm. (VII '01). Transverse section of the genital ridge, showing an indentation (*ind.*) in the ridge. (Sl. 16–3–3. ×200.)

Fig. 2. *Trichosurus vulpecula*, Stage XV *a*, *G.L.* 14 mm. (XI '01). Transverse section of the genital ridge, towards the anterior region, showing a well marked groove (*gr.*) extending in from the coelomic epithelium. (Sl. 20–5–5. ×200.)

Fig. 3. *Trichosurus vulpecula*, *G.L.* 18 mm., *H.L.* 6·75 mm. Transverse section of the genital ridge, showing a hollow invagination (*in.*) from the coelomic epithelium into the rete strands. (Sl. 23–5–10. ×400.)

Fig. 4. *Trichosurus vulpecula*, *H.L.* 9–10 mm. Transverse section of the anterior end of the rete ridge (*r.r.*). The anterior end of the rete (*r.c.*) is seen to lie close against the walls of the Malpighian corpuscles (*gl.*). (Sl. 2–3–4. ×200.)

Fig. 5. *Trichosurus vulpecula*, *H.L.* 11 mm. ♀ Transverse section through the mesovarium, showing the sprouts (*spr.*) from the rete cords (*r.c.*), which extend out to unite with the walls of the Malpighian corpuscles (*gl.*) of the mesonephros. The latter have not as yet undergone degeneration. *spr.gl.* a short outgrowth which has probably arisen from the wall of the Malpighian corpuscle itself to meet the rete sprout. (Sl. 11–3–8 and 7. ×200 and reduced by ¼.)

Fig. 6. *Didelphys aurita*, *H.L.* 10·5 mm. ♂ Transverse section (composite) through the anterior end of the mesonephros. The rete (*r.c.*), which is still a solid cord at its cranial end, is seen to be connected with the M. corpuscles of tubules 2 to 5 of the mesonephros. In the second tubule the position of the former glomerulus (*gl.* 2) is marked by a swelling of the tube, whilst the hinder glomeruli (*gl.* 3, 4, and 5) are in progressive stages of degeneration. The most anterior tubule (*t.* 1) is shown united with the Wolffian duct (*W.D.*); its glomerulus has completely disappeared. The tubule is connected with the rete cord just in front of these sections. *M.D.* Müllerian duct. (Sl. 9–3–1 to 3. ×130 and reduced by ¼.)

Fig. 7. *Perameles nasuta*. *G.L.* 6·8 mm. (13–VII–05). Three consecutive transverse sections through the urogenital fold, right side, immediately in front of the 13th spinal ganglion, showing a developing mesonephric tubule. The wall of that portion of the tubule destined to become the Malpighian corpuscle (*p.M.c.*) is connected with the coelomic epithelium by a rudimentary nephrostome (*a* and *b*, *nph.*), which is united by a band of cells (*c*, *x.*) with the hinder end of the suprarenal primordium (*sr.*), *a.* anterior, *c.* posterior. (Sl. 8–8–13 to 15. ×200.)

Fig. 8. *Idem.* Transverse section through the urogenital fold and a mesonephric tubule of the left side, on a level with the 14th spinal ganglion. That portion of the tubule destined to become the Malpighian corpuscle (*p.M.c.*) is connected with the coelomic epithelium by a thick mass of cells, the rudimentary nephrostome (*nph.*), incompletely separated from the surrounding mesenchyme. (Sl. 8–9–11 and 12. ×200.)

AN INTERPRETATION OF THE RECORDED ARTERIAL ANOMALIES OF THE HUMAN LEG AND FOOT[1]

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During the course of an investigation into the development of the arteries of the human lower extremity, I became very much interested in the study of such published figures of arterial anomalies as happened to be available at the time. Some of these figures revealed the presence in the adult limb of vessels which, from their course and connections, were clearly recognisable as persisting embryonic arteries.

The occasional persistence of such arteries in adult life suggested that a more thorough study of the literature relating to anomalies might well be used for controlling the conclusions already reached by purely embryological means.

Since the direct study of human embryology is so closely dependent upon the accessibility of suitable material, the value of any method, however indirect it may be, which is capable of furnishing evidence bearing upon the nature of developmental process, is too great to be ignored.

In many cases a conception of the type of arterial distribution characteristic of any given stage of development must, of necessity, be founded upon the study of a single embryo. Under the most favourable conditions the data gathered from one specimen may be supplemented by comparison with other embryos representing an approximately identical stage of development. Generally speaking, however, the total number of embryos examined is far too small to provide unequivocal evidence upon the nature of the numerous changes occurring throughout the course of development.

The examination of the literature from which the present paper has resulted was primarily directed towards the recognition of the specific deviation from the course of normal development underlying the production of the particular anomaly investigated. It consists, to a large extent, of an analysis of the many excellent figures which have been published between the year 1743 and the present day. Unillustrated descriptions have been used also, but to a much more limited extent, since the intelligibility of many of the records belonging to this class is vitiated by errors of interpretation and by the omission of essential details.

[1] An essay, substantially identical with the portion of this paper relating to the leg, was accepted by Durham University in partial fulfilment of the requirements for the degree of Doctor of Medicine.

The system of interpretation is based entirely upon the results of the embryological investigation, previously mentioned, which will be published elsewhere[1]. It may be added that the examination of the rather long series of recorded anomalies which forms the basis of this study has not led to the essential modification of any of the opinions expressed in the paper dealing with the process of development.

The sources from which the anomalies examined were taken are noted in the text, but reproductions of line drawings, prepared by means of tracings taken from photographs of the originals, have been added for convenience of reference.

Since it is impossible to name anomalous arteries according to the nomenclature ordinarily applied to the normal adult, *a system has been employed of labelling the normal embryonic components of the abnormal vessels in Roman type.* Persisting embryonic arteries regarded as foreign to normal development, normal adult arteries and other adult structures have been labelled in *Italics.* As a key to the system used, the popliteal and posterior crural regions of a normal leg have been labelled on similar principles and reproduced as fig. 31 (p. 161).

The majority of the figures used have been taken from the following publications[2]:

Tiedmann, F. *Tabulae Arteriarum.* Carlsruhe, 1822.

Bourgery et Jacob. *Traité Complet de l'Anatomie de l'Homme*, tome iv. Paris, 1835.

Quain, R. *The Anatomy of the Arteries of the Human Body.* London, 1844.

Dubrueil, J. M. *Des Anomalies Artérielles.* Paris, 1847.

Hyrtl, J. "Ueber normal und abnorme Verhältnisse der Schlagadern des Unterschenkels," *Denkschriften der Mathematische-Naturwissenschaftliche Classe der K. Akademie der Wissenschaften.* Wien, 1864.

Barkow, H. C. L. "Erläuterungen Zur Schlag—und Blutader—Lehre des Menschen," *Comparative Morphologie des Menschen und Menschenähnlichen Thiere*, Theil vi. Breslau, 1868.

Of the three sections into which the following paper is divided, the second is devoted to the interpretation of the anomalies forming the basis of this study. The shorter section which precedes it reviews the principal changes occurring during the course of normal development. The final section deals with the share taken by each of the embryonic arteries in the composition of the adult arterial system, whether normal or abnormal, and serves as a summary of the other two.

I take this opportunity of acknowledging my obligation to Professor Howden, and to Doctors R. J. Gladstone and Stuart Tidey for their kindness in reading the manuscript and for their helpful criticism.

[1] "On the Development of the Arteries of the Human Lower Extremity," by H. D. Senior, *Am. Journ. Anat.* On account of the large amount of material which has been awaiting publication this paper is not yet in type.

[2] Siebold, R., *Ueber den anomalen Ursprung und Verlauf der in chirurgischer Beziehung wichtigen Schlagaderäste*, Würsburg, 1837, is inaccessible. The sources of anomalies cited from journals and other publications are noted elsewhere.

A BRIEF SKETCH OF DEVELOPMENT

A description of the arterial system of the human lower extremity in progressive stages of its development is to be found in the paper upon development to which reference has been made in the Introduction. The same paper also contains a brief account of each of the embryonic arteries as far as its history has been investigated.

For convenience of reference the main features of the developmental processes involved in the production of the adult arterial system of the leg and foot have been recapitulated here. Further details bearing upon the developmental changes concerned in the production of a few special anomalies are to be found in the section dealing with the region to which the anomaly in question belongs.

The *primitive axial artery*, which arises from the dorsal (secondary) root of the *a. umbilicalis*, already traverses the axis of the limb at an extremely early stage of development. So early, indeed, that the lumbo-sacral nerves have not yet emerged from the spinal medulla, and the limb-bud itself is still indistinctly circumscribed upon the surface. The artery terminates in the region of the foot by dividing into the stem branches of the plantar arterial rete, and into two or three arteries which later blend to form the *r. perforans tarsi*. The latter vessels traverse the sinus tarsi to enter into the formation of the dorsal arterial rete of the foot. Up to *the stage of* 12 *mm.* (fig. 1) the arterial system of the leg retains, in an essentially unaltered condition, the form it presents at 6 mm., the earliest stage at which it has been carefully studied.

During the earlier stages of development there are no means of determining the exact relations borne by the axial artery to the, as yet undifferentiated, skeletal and muscular structures of the part. Throughout the period occupied by its gradual differentiation, the skeletal core of the limb is enveloped by an ill-defined condensation of mesenchyme representing the developing musculature. It is not until a stage of about 18 mm. that differentiation is sufficiently advanced for the identification of the mesenchymal territories which, up to that time, have but virtually represented the individual muscles. Owing to the fortunate circumstance that all the nerves and supporting structures of the limb are clearly recognisable before any part of the axial artery has disappeared, the course of that vessel can be accurately ascertained. It is as follows:

Leaving the pelvis at the distal margin of the m. pyriformis the axial artery follows the n. tibialis as far as the proximal margin of the m. popliteus. Having passed between the m. popliteus and the tibia, it runs between the m. tibialis posterior and the interosseous membrane (figs. 1, 2 and 3). A short distance above the malleoli the artery emerges upon the lateral side of the m. tibialis posterior and closely follows the lateral side of the tendon of that muscle in its course around the medial malleolus. It finally passes into the sole and ends at the plantar orifice of the sinus tarsi.

Before the *stage of* 14 *mm.* (fig. 2), two arterial landmarks have been established which may be used for the convenient subdivision of the axial artery into three sections. These landmarks are the termination of the a. femoralis and the origin of a vessel which represents the first step in the development of the adult a. tibialis anterior, namely, the *r. perforans cruris.*

The section of the axial artery included between the points above indicated will be referred to henceforth as the a. poplitea profunda, while the sections proximal and distal to the a. poplitea profunda will be called the a. ischiadica, and the a. interossea, respectively.

The *a. ischiadica* having previously relinquished the chief blood supply of the limb in favour of the a. femoralis, is represented at the stage of 22 mm. by the *a. glutea inferior*, and by the anastomosing ramifications of the *aa. perforantes* upon the posterior aspect of the m. adductor magnus.

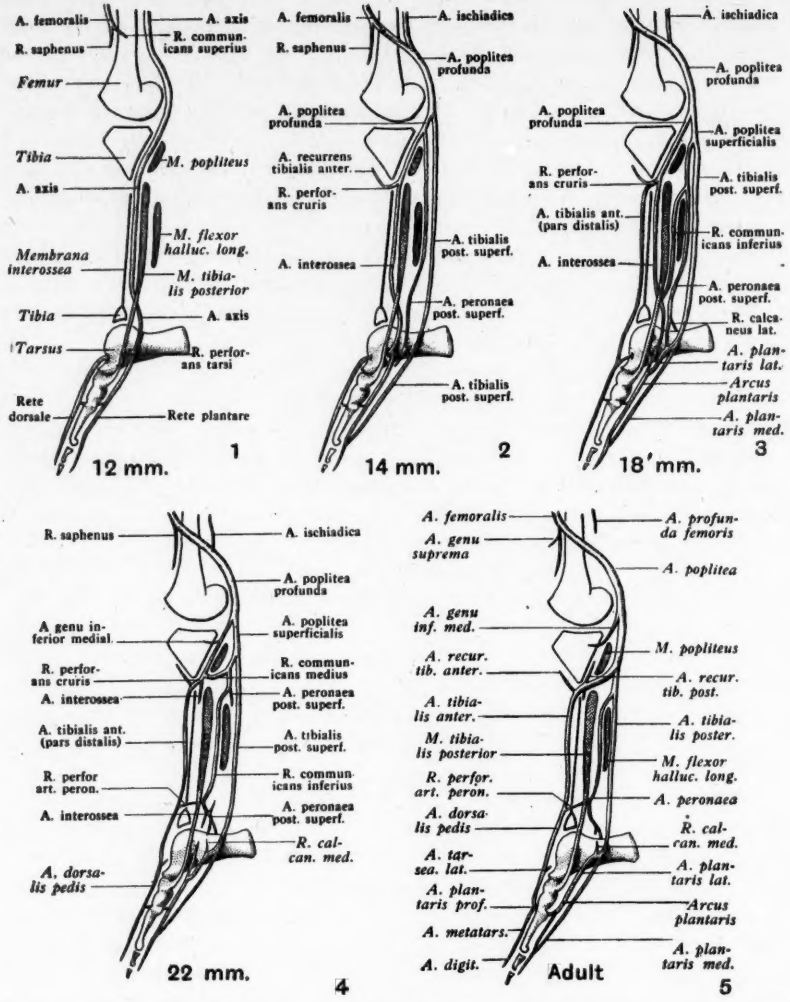
The *a. poplitea profunda* is the most permanent section of the axial artery. The portion of this vessel extending from the hiatus tendineus to the proximal border of the m. popliteus persists unchanged in the adult. The distal portion of the artery, which extends from the proximal border of the m. popliteus to the proximal end of the tibio-fibular interspace and passes anterior to the m. popliteus, has been supplanted at the stage of 22 mm. by the a. poplitea superficialis, which lies upon the posterior surface of that muscle.

The *a. interossea* disappears almost entirely before the completion of development. A short section of it participates, however, in the formation of the supramalleolar portion of the a. peronaea of the adult. The persisting section of the a. interossea gives origin to two important branches which, persisting with it, are taken over branches of the portion of the adult artery. One of the two branches of the a. interossea, the r. coronarius malleolaris, is present at the stage of 18 mm.; the other, the r. perforans, has not been observed until the stage of 22 mm.

At *the stage of* 18 *mm.* the presence of the a. femoralis in the thigh, and the addition of four longitudinal arteries in the leg (making five in the latter situation), has given rise to an arterial arrangement of much greater complexity than that found in the embyro of 14 millimetres.

One of the five arteries which pursue a longitudinal course through the leg at the stage of 18 mm. is the a. interossea, already described. The other four are the a. tibialis posterior superficialis, the a. peronaea posterior superficialis, the r. communicans inferior and the a. tibialis anterior, pars distalis.

The *a. tibialis posterior superficialis* and the *a. peronaea posterior superficialis* are already present at the stage of 14 mm. (fig. 2), at which stage they take independent origin from the a. poplitea profunda. The former artery traverses the leg upon the posterior aspect of the n. tibialis and enters the foot as the *a. plantaris medialis*, while the latter courses to the medial malleolus upon the posterior aspect of the m. flexor hallucis. The a. peronaea posterior superficialis terminates by dividing into two branches which end blindly at the stage of 14 mm. By the stage of 18 mm. (fig. 3) the terminal



Figs. 1–5. Diagrams indicating the distribution of the main arteries of the right leg and foot at four stages of development and in the adult. A sagittal section is represented as having passed through the femur and through the interosseous membrane and adjacent parts of the extremities of the tibia. The section does not involve the skeleton of the foot, which is shown entire. The muscles remain indifferentiated prior to the stage of 18 mm. The positions of the muscles shown in the earlier stages are, therefore, virtual only and not actual.

Labels in Roman type refer to embryonic arteries; italics are used for adult arteries and for all other structures.

branches of this artery have formed a continuous channel which unites the a. tibialis posterior superficialis with the lateral region of the plantar arterial rete. This channel is the *a. plantaris lateralis.*

The a. peronaea posterior superficialis gives origin, at the stage of 18 mm., to a branch which eventually becomes the terminal portion of the a. peronaea, it is the *r. calcaneus lateralis.*

The *r. communicans inferius,* which is a vessel of recent origin at the stage of 18 mm. (fig. 3), eventually takes a large share in the formation of the a. peronaea. Leaving the a. peronaea posterior superficialis on a level with the proximal end of the m. flexor hallucis longus, it passes anterior to the muscle and joins the a. interossea in the supramalleolar region.

The *a. tibialis anterior, pars distalis* arises at a stage of 15–16 mm. from the *r. perforans cruris* which itself appears shortly before the stage of 14 mm. Having followed a course through the anterior crural region identical with that taken by the adult a. tibialis anterior, it joins the dorsal arterial rete of the foot (fig. 3).

At *the stage of* 22 *mm.* two of the arteries of the leg, the a. tibialis anterior and the a. peronaea, have begun to assume their adult form.

The *a. tibialis anterior* has reached completion through the appearance of the *r. communicans medius,* which becomes its definitive root. The embryonic components of the a. tibialis anterior are: The r. communicans medius, a short section of the a. poplitea profunda, the r. perforans cruris, and the pars distalis (see figs. 1—5).

From the time of the appearance of the r. communicans medius, which receives its blood from the developing a. peronaea, the distal end of the a. poplitea profunda begins to undergo retrogression. The a. recurrens tibialis posterior and the root of the a. genu inferior medialis are its representatives in the adult.

The *a. peronaea* has become recognisable mainly by reason of the disappearance of the transient portions of the a. peronaea posterior superficialis and a. interossea. Through extensive degeneration the two latter vessels have relinquished their original connection with the arterial retia of the foot. These are now supplied by the aa. tibialis anterior and posterior.

The embryonic components of the a. peronaea are: The a. peronaea posterior superficialis, the r. communicans inferior, a short section of the a. interossea and the r. calcaneus lateralis of the a. peronaea posterior superficialis. More detailed information regarding the composition of the a. peronaea is given on p. 150.

At this stage of development the a. peronaea arises from the a. poplitea superficialis and gives origin to the a. tibialis anterior.

The *arterial arrangement of the adult leg* differs from that encountered at the stage of 22 mm. mainly in the completion of the a. poplitea, and in the origin from that vessel of the a. tibialis anterior.

The formation of the *adult a. poplitea* has been accomplished by the blending

of the proximal part of the a. poplitea profunda with the *a. poplitea superficialis*. The latter vessel, which arises through the gradual union of the proximal part of the a. peronaea posterior superficialis with that of the a. tibialis posterior superficialis, lies upon the posterior surface of the m. popliteus. By the time the a. poplitea has reached completion it has taken over the a. tibialis anterior as one of its terminal branches.

The progressive union between the a. peronaea posterior superficialis and the a. tibialis posterior superficialis does not stop at the termination of the a. poplitea. It is continued as far as the point at which the adult a. peronaea takes origin from the *a. tibialis posterior*.

The part of the a. tibialis posterior distal to the origin of the a. peronaea is derived directly from the a. tibialis posterior superficialis. It differs from its embryonic precursor, however, in the relation it bears to the n. tibialis.

ANOMALIES IN THEIR RELATION TO ARTERIAL DEVELOPMENT

It is questionable whether even the most local deviation from the course of normal arterial development manifests itself entirely within the limits of a single adult artery. Cases characterised by absence, or other gross variation, of one of the adult arteries are commonly classified as anomalies of the particular vessel most obviously affected. In consequence, however, of the very intimate interdependence of the alternative arterial routes which successively become available during the progress of development, it happens that arterial anomalies affect general arterial regions rather than individual vessels.

The classification used in this paper depends upon the selection of three general regions in the leg, and the treatment of the foot as a whole. The leg regions (particularly the first and third) are somewhat arbitrarily separated, but have been found convenient in practice. They are the popliteal, the anterior crural and the posterior crural.

In analysing cases in which the anomaly depends upon the absence of one of the embryonic arteries it has been assumed, unless there is evidence to the contrary, that the absence is primary, and not due to the disappearance of a vessel once present. In cases in which neither alternative is subject to verification the first, and perhaps the more probable of the two, has been taken for granted in order to obviate the necessity of repeating the possibilities of each case.

A. THE POPLITEAL REGION

The only section of the embryonic axial artery which normally persists as a main adult trunk is that represented by the part of the a. poplitea profunda which furnishes the part of the adult a. profunda extending from the hiatus tendineus to the origin of the a. genu medialis inferior. The section of the adult a. poplitea in question seems to be invariable even though its proximal and distal connections may be quite abnormal. The portion of the

embryonic a. poplitea profunda which lies anterior to the m. popliteus, normally abandons its original function as part of the main arterial channel into the leg, and is superseded by the a. poplitea superficialis which passes posterior to that muscle.

The recorded anomalies of this region are as follows:

1. HIGH DIVISION OF THE POPLITEAL ARTERY INTO THE POSTERIOR TIBIAL AND PERONEAL, THE LATTER GIVING OFF THE ANTERIOR TIBIAL: fig. 6, from Quain (pl. 79, fig. 5). Examples of an exactly similar anomaly have been given by Haller (*Icones Anatomicae*, Göttingen, 1743, pl. 5) and Tiedmann (pl. 51, fig. 3). Others, by Barkow and Hyrtl, are reproduced here as figs. 25 and 26.

The a. poplitea superficialis is absent, the embryonic a. tibialis posterior superficialis and a. peronaea posterior superficialis having failed to unite in the normal manner.

Failure in the union of the roots of these two embryonic arteries has produced a further anomaly which affects the aa. tibialis posterior, peronaea, and tibialis anterior. The first of these arteries is necessarily smaller than usual above the point at which a. peronaea should normally arise. The a. peronaea, instead of arising from the a. tibialis posterior, takes origin from the a. poplitea, while the a. tibialis anterior arises from the a. peronaea.

2. HIGH ORIGIN OF THE PERONAEAL ARTERY, THE POPLITEAL BEING NORMAL: fig. 7, from Quain (pl. 79, fig. 6). This anomaly, though slighter in degree, is of precisely the same nature as the preceding. Union between the aa. peronaea posterior superficialis and tibialis posterior superficialis has failed to extend as far as usual. The failure has resulted in diminution of the calibre of the proximal part of the a. tibialis posterior. The proximal part of the a. tibialis anterior (r. communicans medius) arises from the a. peronaea, as in the embryo of 22 mm. (fig. 4).

3. HIGH DIVISION OF THE POPLITEAL ARTERY INTO POSTERIOR AND ANTERIOR TIBIAL: fig. 8, from Quain (pl. 79, fig. 3). This anomaly would appear to depend upon a series of events more complicated than that underlying the two preceding cases. Union between the embryonic aa. peronaea posterior superficialis and tibialis posterior superficialis, instead of being complete as far as the site of origin of the future a. peronaea, seems to have occurred in the region near the distal margin of the m. popliteus only.

The greater part of the blood entering the proximal part of the a. peronaea posterior superficialis would, under such circumstances, have passed through the r. communicans medius which ordinarily forms the root of the a. tibialis anterior. The greater part of the blood entering the proximal part of the a. tibialis posterior superficialis would, similarly, have passed into the distal part of the vessel. A smaller proportion of the blood entering the proximal part of each vessel would be free to enter the distal part of the a. peronaea posterior superficialis.

The transition from such an arrangement to the condition of affairs repre-

sented in fig. 8 could be readily explained by assuming the subsequent disappearance of the part of the a. peronaea posterior superficialis which originally intervened between the origin of the r. communicans medius and its junction with the a. tibialis posterior superficialis. The disappearance of the part of the vessel in question would leave the r. communicans medius attached to the proximal part of the a. peronaea posterior superficialis. The distal part of the latter artery would remain attached to the a. tibialis posterior superficialis and become the root of the adult a. peronaea.

4. HIGH DIVISION OF THE POPLITEAL ARTERY, THE ANTERIOR TIBIAL ARTERY PASSING ANTERIOR TO THE POPLITEUS MUSCLE: fig. 9, from Quain (pl. 79, fig. 4). This anomaly depends upon absence of the embryonic r. communicans medius, which, in normal cases, forms the root of the adult a. tibialis anterior. The deficiency has been rectified by the maintenance of the connections normally found at the embryonic stage of 18 mm. The distal part of the a. poplitea profunda has retained its integrity and supplies the anterior crural region by transmitting blood directly into the r. perforans cruris.

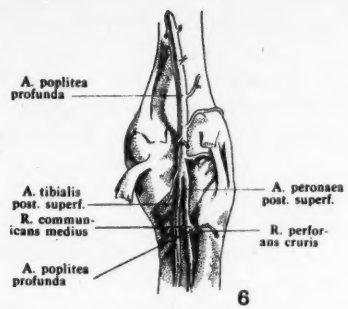
5. DIVISION OF THE POPLITEAL ARTERY INTO ANTERIOR TIBIAL AND "GREAT" PERONAEAL, OR AN ARTERY DERIVED FROM KINDRED ANTECEDENTS, THE POSTERIOR TIBIAL BEING ABSENT: figs. 21, 22, 23 and 24. Further examples of the anomaly represented in fig. 21 are recorded by Quain (pl. 84, fig. 3), Tiedmann (pl. 36, fig. 3) and Hyrtl (pl. 3, figs. 1 and 2). All these cases are characterised by absence of the embryonic a. tibialis posterior superficialis as will be discussed later. The proximal portion of the a. poplitea has been formed, in the usual way, from the a. poplitea profunda, while the distal portion may be regarded approximately as a direct survival of the root of the embryonic a. peronaea posterior superficialis.

6. FIGURES OF TWO SO-CALLED ANOMALIES OF THE POPLITEAL ARTERY, WHICH SEEM TO BELONG ONLY SECONDARILY TO THIS VASCULAR REGION, ARE REPRODUCED AS FIGS. 10 AND 11, from Hyrtl (pl. 1, figs. 1 and 2).

In each there is an artery which, lying upon the lateral side of the a. poplitea, inosculates with that vessel near the back of the knee joint. The proximal part of the artery in question (a. commitans nervi ischiadici in the first case, and the a. perforans tertia in the second) is clearly a persisting part of the a. ischiadica.

The embryonic a. ischiadica normally terminates at the hiatus tendineus by becoming the a. poplitea profunda. The distal portion of the anomalous artery in both of Hyrtl's cases is, therefore, not a part of the a. ischiadica. It appears to be merely an anastomosing muscular ramus of the a. poplitea. If these cases are to be regarded as anomalies of the a. poplitea at all, they should be classed as secondary rather than primary anomalies of that vessel.

The primary nature of another case published by Hyrtl, and cited by Krause as an anomaly of the a. poplitea (Henle's *Gefässlehre*, p. 305) may also be regarded as somewhat questionable. In the case in question the a. suralis



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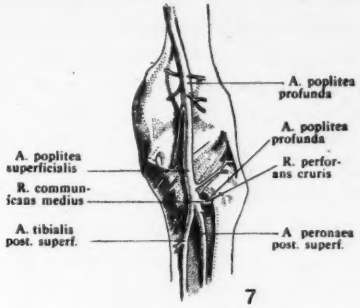

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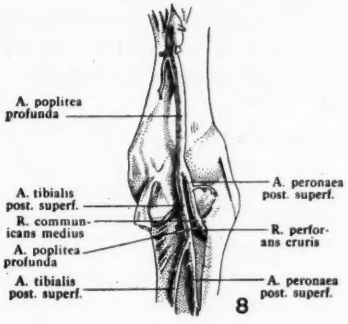

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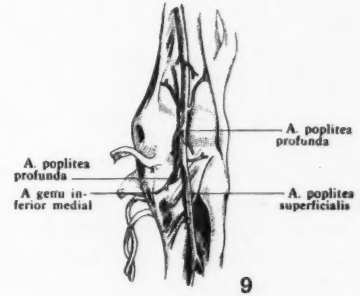

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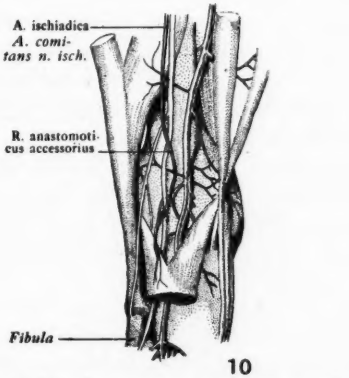

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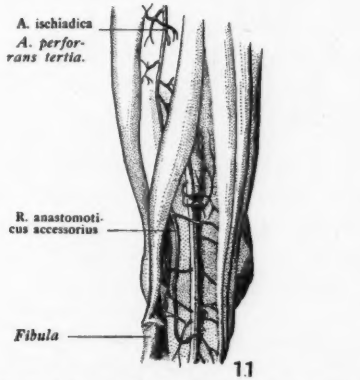

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Figs. 6–11. The anomalies shown in figs. 6, 8 and 9 affect the popliteal, peronaeal and anterior and posterior tibial arteries. In the case of fig. 7 the same arteries, with the exception of the popliteal, are involved. Figs. 10 and 11 represent a persisting ischiadic artery, the original termination of which has been supplanted by a new, and more distal, connection with the popliteal.

Labels in Roman type refer to the normal embryonic predecessors of the adult arteries shown; italics are used for all other structures. Figs. 6–9 from Quain, pl. 79, figs. 5, 6, 3 and 4 respectively: 10 and 11 from Hyrtl, pl. 1, figs. 1 and 2 respectively.

magna arises from the a. poplitea. Hyrtl's figure (pl. 3, fig. 3), which has been reproduced here as fig. 29, will be referred to again in the section devoted to the anomalies of the posterior crural region.

The embryonic elements entering into the composition of the a. tibialis anterior in the cases reproduced as figs. 6, 7, 8 and 9, are reviewed, together with those found in other anomalies affecting that vessel, on the next page.

B. THE ANTERIOR CRURAL REGION

The portion of the a. tibialis anterior situated in this region of the leg is the product of two embryonic vessels, namely, the r. perforans cruris and the a. tibialis anterior, pars distalis. Of these, the former appears to be absolutely constant, while the latter is not infrequently too small for the complete arterial supply of the dorsum of the foot, and may be altogether absent. Very occasionally the anomalous a. saphena magna appears as an accessory vessel in this region and reaches the malleoli. It may even be large enough to assist materially in the arterial supply of the foot.

The graphically recorded anomalies of the anterior crural region are as follows:

7. THE DISTAL PART OF THE ANTERIOR TIBIAL ARTERY IS ABSENT: fig. 12, from Hyrtl (pl. 8, fig. 2). In this case arterial blood is conveyed to the dorsum of the foot by a branch of the a. tibialis posterior which perforates the interosseous membrane at the junction of the middle and lower thirds of the leg.

From the large size of the a. dorsalis pedis, as compared with the perforating branch, it is obvious that the former vessel receives the greater proportion of its blood from the arcus plantaris by way of the r. plantaris profundus. The r. perforans cruris, and its continuation the a. recurrens tibialis anterior, have retained the relations normally found in the embryo of 14 mm. (fig. 2).

The a. tibialis anterior, pars distalis, which should have been developed later (fig. 3), has failed to appear, or, having appeared, has undergone partial degeneration. The large recurrent branch which passes from the perforating ramus towards the r. perforans cruris suggests the probability of the latter alternative. No other figures of this anomaly have been found in the literature. Similar cases, however, have been recorded by Burns (*Diseases of the Heart*, 1809), Ryan (*Diss. Inaug. de quarundam Arteriarum in Corpore Humano Distributione*, 1812), and Otto (*Pathol. Anat.* 1829).

8. THE DISTAL PART OF THE ANTERIOR TIBIAL ARTERY IS SMALL: fig. 13, from Quain (pl. 85, fig. 5). In this example the a. tibialis anterior ends, without inosculation, among the extensor muscles of the leg. The a. dorsalis pedis arises from a large r. perforans arteriae peronaeae. Dubrueil, also, figures a somewhat similar case (pl. 17, fig. 2).

Cases in which a small a. tibialis anterior is sufficiently long to inosculate with, and be reinforced by, the r. perforans have been figured by Tiedmann (pl. 36, fig. 2), Quain (pl. 85, fig. 4), Hyrtl (pl. 8, fig. 1), Barkow (pl. 9, figs. 1, 2 and 3; pl. 10, figs. 1 and 2) and others. Numerous unillustrated instances

in which the r. perforans (with or without inosculation with an a. tibialis anterior of small size) had provided the main arterial supply of the dorsum of the foot, are scattered throughout the literature. The anomaly is of common occurrence.

Anomalies affecting the anterior tibial artery occur not only in the anterior crural, but in the popliteal region also.

The a. tibialis anterior is the product of four embryonic arteries which arise at different stages of development. The part of the adult artery which takes origin from each of the embryonic vessels concerned can be identified with approximate accuracy, as follows:

Part I extends from the origin of the artery to a point immediately proximal to the origin of the a. recurrens tibialis posterior. It corresponds to the whole of the embryonic r. communicans medius.

Part II is the part of the artery which gives origin to the a. recurrens tibialis posterior, and, occasionally, to a short descending branch which represents a persisting part of the a. interossea. This part of the artery is derived from a very small section of the embryonic a. poplitea profunda.

Part III extends from a point immediately distal to the origin of the a. recurrens tibialis posterior to the origin of the a. recurrens tibialis anterior. It is derived from the embryonic r. perforans cruris.

Part IV extends from the distal side of the origin of the a. recurrens tibialis anterior to the front of the ankle joint. It corresponds to the entire a. tibialis anterior, pars distalis, of the embryo.

In the anomaly shown in fig. 6, the embryonic elements which enter into the formation of the a. tibialis anterior are five in all, viz. the a. peronaea posterior superficialis, r. communicans medius, a. poplitea profunda, r. perforans cruris, and the pars distalis. The same elements appear in the anomalies shown in figs. 7 and 8, but in the former case the part contributed by the a. peronaea posterior superficialis is much shorter than that found in the cases which form the subjects of figs. 6 and 8.

In the anomalies shown in fig. 9 the embryonic components of the a. tibialis anterior are: the a. poplitea profunda, r. perforans cruris, and the pars distalis; in that of fig. 12, they are the r. communicans medius, a. poplitea profunda (presumably), and the r. perforans cruris; three in each case. In the case of fig. 13, the embryonic components are normal in number and order, but the fourth has failed to reach its usual goal, namely the rete dorsale pedis.

An anomaly of the anterior tibial artery, apparently unique but much quoted in the literature, is that of Velpeau (*Eléments de Médicine Opératoire*, 1839) of which no figure is given. In this case the artery is recorded as having reached the anterior crural region by passing laterally around the neck of the fibula, following the course of the n. peronaeus communis. Such an artery is not of normal occurrence in the embryo, and must be regarded as peculiar to the individual in which it occurred. The embryonic elements entering into

the formation of the a. tibialis anterior in Velpeau's case may be supposed (in the absence of a figure showing the exact conditions) to have been as follows: a. comitans n. peronaei, a. recurrens tibialis anterior, r. perforans cruris, and the pars distalis. It may be supposed, further, that the r. communicans medius, the portion of the r. perforans cruris posterior to the interosseous membrane, and the portion of the a. poplitea profunda which normally unites them, were absent. The two latter components of the anomalous vessel, which must have been present in their respective stages of development, were presumably lost in consequence of usurpation of function. The former (not necessarily present at all) may have failed to develop as in the case illustrated in fig. 9.

9. A. SAPHENA MAGNA: fig. 14, from Zagorski (*Mémoires de l'Académie Impériale des Sciences de St Pétersbourg*, T. I. 1809).

Two figures have been published which very closely resemble Zagorski's, namely, those of Barkow (pl. 56, fig. 1) and Manners-Smith (*Journ. Anat. and Physiol.* vol. XLV. pl. 20). In all three the origin of the a. saphena is independent of that of the common trunk of the musculo-anastomotic rami, a condition found in the embryo prior to the stage of 22 mm.

Unillustrated instances have been reported by Broca (*Bulletin de la Soc. Anat.*, Paris, 1849), Rug, and Popowski. Rug's case occurred in association with persistence of the embryonic a. ischiadica (*Würzburger Medicinische Zeitsch.*, Bd. IV. 1863). The thigh only appears in the figure, which, however, shows the root of an unusually large a. genu suprema.

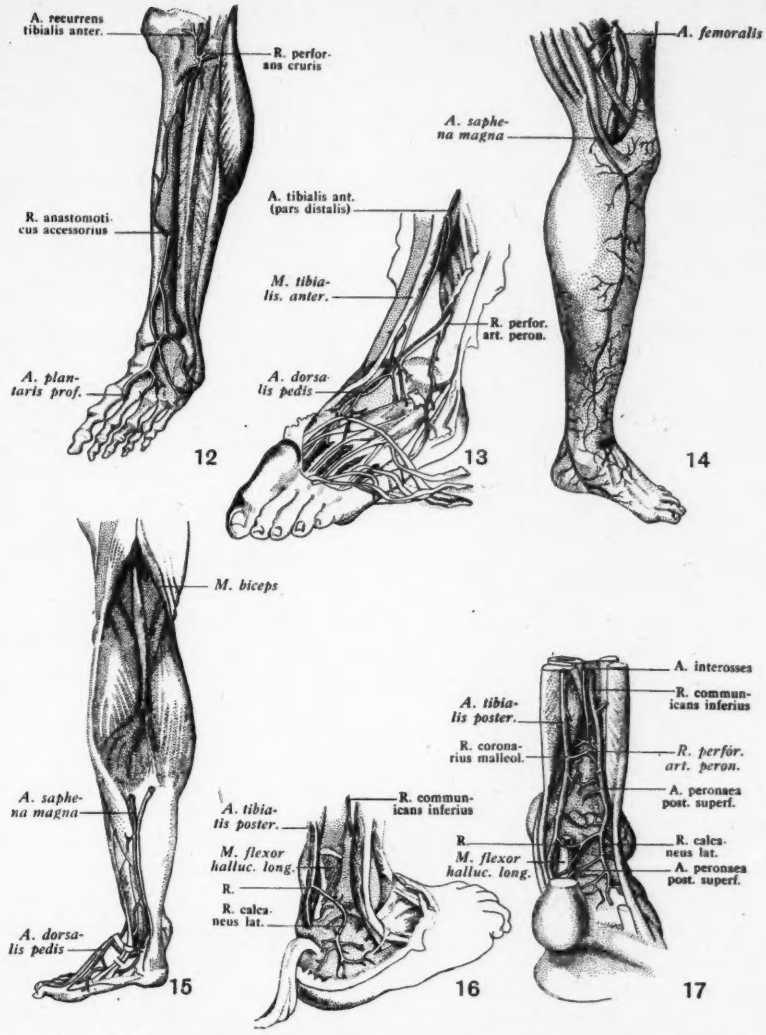
Judging from Rug's description the ultimate distribution of the main trunk of the vessel resembled the a. saphena magna of Zagorski's example.

In Popowski's case (*Anatomischer Anzeiger*, Bd. VIII. 1893) the artery, of which the root is as large as the a. poplitea, has a very much more extensive distribution. It divides into an anterior and a posterior branch, the former of which extends to the foot to supply the medial side of the great toe and reinforce the a. dorsalis pedis, while the posterior branch passes beneath the calf muscles to reinforce the a. tibialis posterior.

Fig. 15, from Hyrtl (pl. 3, fig. 3), represents an interesting case of a. saphena magna occurring in the right leg of a new-born infant. In this instance the vessel does not arise from the a. femoralis, but from the a. tibialis posterior.

Hyrtl's case would admit of a relatively simple explanation, and not improbably the true one, if it were assumed that the a. saphena magna originally resembled the large vessel described by Popowski. The posterior branch of such an artery, if it should have transmitted blood from the a. tibialis posterior into the anomalous artery, rather than in the contrary direction, might well have usurped the function of the original root of the a. saphena magna. It is unfortunate that the limb was not posed, for the purpose of reproduction, in such a way as to display the region of the a. femoralis from which the a. genu suprema usually takes origin.

The small branch of the a. saphena magna shown in fig. 15, which passes



Figs. 12–17. The chief anomaly in figs. 12 and 13 is of the anterior tibial artery. Subsidiary anomalies affect the posterior tibial and dorsalis pedis in the former, and the peronaeal in the latter. Figs. 14 and 15 are examples of a. saphena magna. The peronaeal and posterior tibial arteries are anomalous in fig. 16, and the peronaeal in fig. 17.

Labels in Roman type refer to the normal embryonic predecessors of the adult arteries shown; italics are used for all other structures. Figs. 12 and 15 from Hyrtl, pl. 8, fig. 2, and pl. 4, fig. 2 respectively; fig. 14 from Zagorski; figs. 13 and 16 from Quain, pl. 85, fig. 5, and pl. 84, fig. 4 respectively; fig. 17 from Tiedmann, pl. 36, fig. 4.

anterior to the malleolus, represents, no doubt, the true termination of the artery. Nevertheless, the behaviour of the termination of the main trunk in Hyrtl's case bears a very striking resemblance to that of the anterior branch in Popowski's. It divides into two branches, one of which supplies the medial border of the great toe, while the other passes laterally beneath the tendons of the mm. tibialis anterior and flexor hallucis longus to join the a. dorsalis pedis.

It would appear, on the whole, that what may be regarded as the fully developed termination of the a. saphena magna finds exemplification in the case of Popowski and Hyrtl rather than in those of Zagorski and Barkow and Manners-Smith. In the three latter cases the vessel loses its individuality before it reaches the medial malleolus.

Although the anomalous a. saphena magna appears in the anterior crural region, the circumstances bearing upon its origin and proportions form a part of the developmental history of the arteries of the thigh. The *a. iliaca externa*, which arises from the a. umbilicalis before the stage of 8·5 mm., ends blindly until after the stage of 11 mm. It then divides into the *a. epigastrica inferior* and the *a. femoralis*, which grow rapidly into their respective territories. The growing extremity of the a. femoralis is, from the very first, bifurcated into the *r. communicans superius* and *r. saphenus*. The former branch joins the axial artery at the hiatus tendineus shortly after the developmental stage of 12 mm., while the latter, growing into the anterior crural region, extends less than half way down the leg. The musculo-anastomotic ramus of the *a. genu suprema* arises originally from the a. femoralis, but is taken over by the r. saphenus (the root of which thus becomes common to all branches) at the stage of 22 mm.

In Rug's case of a. saphena magna it does not seem unreasonable to suspect correlation between abnormal overgrowth of the r. saphenus and absence of the r. communicans superius. The other examples of this anomaly do not seem to admit of a definite embryological explanation.

Out of a relatively large number of human embryos examined by the writer, in which the a. femoralis had tapped the axial trunk in the normal way, not one was found in which the importance of the r. saphenus approached that of the a. saphena of Popowski, or even those of Zagorski, Barkow and Manners-Smith. The opinion has been expressed by some comparative anatomists[1] that the a. genu suprema and r. saphenus of the human adult probably represent a vestige of a much larger embryonic vessel. A large r. saphenus, appearing at any stage of development, would seem, on the contrary, to be almost as rare an anomaly in the embryo as is the occurrence of an a. saphena magna in the adult.

The arterial supply of the sole by means of the a. saphena occurs throughout

[1] Notably Zuckerkandl, 1895, "Zur Anat. u. Entwickelunges des Unterschenkels u. des Füsses," *Anat. Hefte*, B. 5, H. 2, 207, and Popowski, 1893, "Ueberbleibsel der Arteria saphena beim Menschen," *Anat. Anz.*, B. 8, 580.

the mammalian series with sufficient constancy as to suggest, on purely theoretical grounds, the likelihood of compensation for anomalous absence of the human a. tibialis posterior through the agency of the a. saphena magna. The information yielded by an examination of the graphically recorded instances of the anomaly in question, however, is entirely negative in this regard. It is found, firstly, that compensation has been accomplished in all such cases through the abnormal persistence of the distal part of the embryonic a. peronaea posterior superficialis. Secondly, that persistence of the a. saphena magna in association with absence of the a. tibialis posterior has not hitherto been recorded.

A closer comparison between the part of the a. saphena which normally supplies the aa. plantares in the great majority of mammals, upon the one hand, and the part of the a. peronaea posterior superficialis which supplies the sole in the human anomaly characterised by absence of the a. tibialis posterior, upon the other, may prove to be exceedingly interesting. More accurate information than is now available regarding the course usually followed by the posterior branch of the well-developed mammalian a. saphena magna in its passage through the malleolar region would be necessary for purposes of comparison. It is not improbable that the morphological affinity between the malleolar section of the two arteries may be greater than the nature of their more proximal connections would suggest.

In the cases of Popowski and Hyrtl cited above, the share taken by the a. saphena magna in the dorsal arterial supply of the foot recalls that encountered normally in many other primates. As has been noted above, however, deficient development of the distal part of the human a. tibialis anterior usually receives compensation through proportional enlargement of the a. perforans arteriae peronaeae.

C. THE POSTERIOR CRURAL REGION

Many cases are recorded in the literature in which but one large artery traverses the posterior crural region and supplies the sole. The single artery has been interpreted as the a. peronaea in some such cases and as the a. tibialis posterior in others. The latter interpretation, where made, would seem to have been founded upon the fact of its being the chief artery of the region and supplying the sole, rather than upon information which might have been gained from the study of its relations.

Hyrtl, in commenting (in 1864) upon the great rarity of absence of the a. peronaea, refers to No. 2093 in the Breslau Anatomical Museum as the only undoubted example of this anomaly with which he is acquainted. Krause also, in Henle's *Gefässlehre* (Braunschweig, 1868) cites No. 2095 G in the Breslau Museum, as having the endorsement of Hyrtl, and refers, in addition to No. 2113 of the Göttingen collection.

Barkow's review of the evidence bearing upon the nature of the single large artery which occasionally traverses the posterior crural region and

supplies the sole, is most instructive. It is founded upon an examination of nine examples of this anomaly contained in the Breslau Museum, including those cited by Hyrtl and Krause. Although Barkow's views upon the subject are most guardedly expressed, his evidence does not favour the view that a case has ever been recorded in which the a. tibialis posterior supplied the posterior crural region and sole, in the absence of the a. peronaea[1].

In view of the fact that reliably recorded instances of absence of the a. peronaea do not appear to be available, it is extremely desirable that a good reproduction of any case which appears to be an example of this anomaly should be placed upon record.

That the a. tibialis posterior is not essential for the adequate supply of the foot is indicated by the comparative frequency of its absence from the adult leg. In all cases in which the a. tibialis posterior is absent in adult life, and in some in which it is small, the distal part of the embryonic a. peronaea posterior superficialis, instead of undergoing retrogression, has retained its primitive connection with the a. plantaris lateralis.

In the absence of the a. tibialis posterior, the artery which performs the function of the missing vessel is invariably derived from the embryonic arteries which take part in the formation of the normal adult a. peronaea. In the cases in which the persisting elements of the embryonic vessels in question are identical with those entering into the composition of the a. peronaea, and arranged in a similar order, the main artery of the posterior crural region takes the form of a large peronaeal artery which, instead of ending in the leg, is continued into the sole. Some cases occur, however, in which the persisting portions of the embryonic arteries in question differ somewhat from those

[1] Barkow thinks it probable that the cases cited by Hyrtl and Krause, and those described by Otto and Lauth as examples of absence of the a. peronaea, belong to a single group which includes also the recorded examples of absence of the a. tibialis posterior. In his opinion there is a great general resemblance between all the cases belonging to the Breslau Collection, notwithstanding the fact that the single artery of the posterior crural region has been labelled a. peronaea in some of them, and a. tibialis posterior in others.

The eight Breslau preparations are all dried specimens and bear the numbers XLIX. 14, 15, 16, 17 and 18, and L. 4, 9 and 10 respectively. Hyrtl's case, originally No. XLIX. 16, was renumbered 2093 by Otto. It is somewhat damaged, but, judging from Barkow's description, does not appear to differ materially from the others. The Breslau case cited by Krause as having Hyrtl's endorsement is not really the same as that to which Hyrtl referred; Krause, having evidently transposed the 5 and 9, appears to have been misled by the similarity of numbers. No. 2059 G (Krause's specimen) is a more recent acquisition, and was numbered by Barkow, who described the case as "absence of the peronaeal in which the posterior tibial takes the course of the missing vessel."

Barkow concludes that Krause's Göttingen specimen conforms to the same general type as those belonging to the Breslau collection. This conclusion appears to me to be borne out by Krause's statement (p. 310) that the a. perforans arteriae peronaeae arises, in his specimen, from the a. tibialis posterior. The r. perforans is developmentally a branch of the part of the a. interossea which becomes the third portion of the normal a. peronaea. If Krause's perforating branch is really the vessel he takes it for, the artery from which it arises is certainly not the a. tibialis posterior.

See Barkow, H. C. L., *Die Angiologische Sammlung im Anatomischen Museum der Königlicher Universität zu Breslau*, Breslau, 1869.

which enter into the formation of the normal a. peronaea. The embryonic structure of the artery which traverses the posterior crural region, in cases of this kind, to supply the sole, may vary very considerably in detail.

In spite of variations occurring in the embryonic composition of the artery which may replace the a. tibialis posterior as the chief artery of the posterior crural region, one part of it remains invariable. The part in question is that which traverses the malleolar region upon the lateral side of the tendon of the m. flexor hallucis longus and passes, anteriorly to that tendon, into the sole. It is the portion of the embryonic a. peronaea posterior superficialis which lies distal to the origin of its r. calcaneus lateralis.

Persistence of the distal part of the a. peronaea posterior superficialis and absence of the adult a. tibialis posterior seem to depend, alike, upon absence of the embryonic a. tibialis posterior superficialis. This point is evident from the developmental history of the connections between the arteries of the leg and those of the foot:

The deeper arteries of the sole, including the arcus plantaris, are derivatives of the original plantar rete, which dates from the developmental period during which the sole is supplied by the a. interossea. The a. plantaris medialis represents the terminal portion of the embryonic a. tibialis posterior superficialis. The a. plantaris lateralis represents the connection between the a. tibialis posterior superficialis and the lateral region of the rete plantare which is effected at the stage of 18 mm., through the agency of the two terminal branches of the a. peronaea posterior superficialis.

In cases in which the a. tibialis posterior superficialis is normally developed, the a. plantaris lateralis conducts some of the blood which issues from the a. tibialis posterior into the rete plantare, the remainder passing into the a. plantaris medialis. In cases, however, in which the a. tibialis posterior superficialis fails to appear, or is too small to reach the sole, the medial terminal branch of the a. peronaea posterior superficialis is unable to form its usual connection. In such cases blood might pass from the leg to the rete plantare either by way of the a. interossea or through the lateral terminal branch of the a. peronaea posterior superficialis.

The distal portion of the first named artery normally disappears shortly after the lateral branch of the a. peronaea posterior superficialis has reached the rete plantare. No case of persistence of the a. interossea in adult life has been recorded. The artery which supplies the sole in all recorded cases of absence of the a. tibialis posterior, is the persisting distal portion of the embryonic a. peronaea posterior superficialis.

It can be readily understood how a vessel formed from persisting sections of the embryonic a. interossea and peronaea posterior superficialis (whether combined as the normal a. peronaea or in some other manner) which, traversing the posterior crural region, might supply the sole in the absence of the a. tibialis posterior. It would be so difficult, however, to account for the presence of the a. tibialis posterior in association with absence of the

a. peronaea, or an artery derived from similar antecedents, that there is little wonder that examples of such an anomaly do not seem to have been recorded.

In order to explain the formation of the arcus plantaris and the a. plantaris lateralis, it is necessary to assume the presence (at their respective stages of development) of the a. interossea and of the a. peronaea posterior superficialis. In order to account for the production of an anomaly in which the sole is supplied by the a. tibialis posterior, in the absence of the a. peronaea (or a vessel derived from its normal embryonic antecedents), it would still be necessary to make a further assumption. It would be necessary, in fact, to assume that the aa. interossea and peronaea posterior superficialis had disappeared at a stage of development subsequent to that in which the material for the development of the chief arteries of the sole had been provided by their branches.

The anomalies graphically recorded as having occurred in the posterior crural region are the following:

10. THE PERONAEAL ARTERY IS SMALLER THAN USUAL, THE POSTERIOR TIBIAL BEING PRESENT: fig. 16, from Quain (pl. 84, fig. 4).

In this case the r. communicans inferius forms the termination of the a. peronaea. The embryonic vessel which normally forms the termination of this adult artery, namely, the r. calcaneus lateralis of the a. peronaea posterior superficialis, figures as a branch of the a. tibialis posterior.

The production of this anomaly appears to depend upon disappearance of the portion of the embryonic a. interossea, which usually persists to form the part of the a. peronaea immediately succeeding the part derived from the r. communicans inferius. The portion of the a. interossea in question, together with the r. coronarius malleolaris and the r. perforans, to which it normally gives origin, is entirely absent.

Fig. 17 from Tiedmann (pl. 36, fig. 4) represents another anomaly characterised by failure of the a. interossea to enter into the formation of the a. peronaea. This case seems to throw light upon the nature of the changes which transform the embryonic pattern of the supramalleolar region into that which characterises the adult. The changes in question are so numerous, and so nearly simultaneous in their occurrence, that they are difficult to follow satisfactorily in the embryo.

In Tiedmann's anomaly the a. interossea is not absent, as in Quain's case, but lies upon the medial side of the a. peronaea. It not only gives off the r. coronarius malleolaris and the r. perforans but effects its normal junction with the distal part of the a. peronaea posterior superficialis. How the a. peronaea has been completed without the interpolation of the usual short section of the a. interossea between the parts contributed by the r. communicans inferius and the a. peronaea posterior superficialis, it does not seem possible to determine with certainty. The main importance of the case lies in the independent co-existence of a persisting section of the a. interossea and of the portion of the a. peronaea which it normally forms.

Another interesting feature of this case is the persistence, although diminished in size, of the portion of the embryonic a. peronaea posterior superficialis which lies beyond the origin of the r. calcaneus lateralis. The part of the embryonic artery in question is connected with the a. tibialis posterior by a branch which effects an indirect communication between that vessel and the a. peronaea.

The persistence of the distal part of the embryonic a. peronaea posterior superficialis and its connection with the a. tibialis posterior clearly explains the mechanism of the transference of the r. calcaneus lateralis to the a. tibialis posterior which has occurred in Quain's case of fig. 16. It seems also to throw light upon the nature of the unnamed branch, so frequently to be seen upon the posterior surface of the m. flexor hallucis longus, which connects the a. tibialis posterior and the a. peronaea. This superficial communicating branch, of which the primitive relations are revealed in fig. 17, has been labelled *R* in figs. 16, 17 and 31.

The superficial connection between the a. peronaea and a. tibialis posterior mentioned above is entirely distinct from the deeper connection between these two vessels known as the r. communicans.

The nature of the r. communicans has been deduced by Hyrtl from an exhaustive examination of its relations in the adult leg. According to Hyrtl (*Schlagadern des Unterschenkels*, 1864, p. 21) the r. coronarius malleolaris of the a. peronaea originally passes across the posterior and medial surfaces of the tibia to join the a. tibialis anterior. Its union with the a. tibialis posterior, which subsequently occurs through anastomosis, divides the r. coronarius into two parts. Of these, the part intervening between the a. peronaea and the a. tibialis posterior becomes the r. communicans, while that extending from the a. tibialis posterior to the a. tibialis anterior is transformed into the aa. malleolares mediales and the rete malleolare mediale.

While the blending of the a. tibialis posterior with the r. coronarius has not been observed in the human embryo, the latter vessel, from the time of its first appearance as a branch of the a. interossea (the a. peronaea not having been formed), follows the course which Hyrtl ascribes to it. At the stage of 22 mm. the a. tibialis posterior is widely separated from the r. coronarius by the n. tibialis. The separation of the two arteries, however, is subsequently so greatly reduced by the assumption of the adult relations between the n. tibialis and the a. tibialis posterior, that there can be little doubt as to the substantial correctness of Hrytl's interpretation.

For the purpose of forming comparisons between the various *anomalies affecting the peronaeal artery* it will be convenient to review the composition of the normally developed artery in terms of its embryonic antecedents. The distinctive relations taken by the adult a. peronaea in the successive stages of its course through the leg provide a basis for the division of this vessel into four parts. The parts in question are derived respectively from the four distinct embryonic elements from which the adult artery has arisen.

The parts of the adult a. peronaea, and the embryonic elements which precede them are as follows:

Part I extends from the origin of the artery to the proximal margin of the m. flexor hallucis longus. It is derived from a persisting section of the embryonic a. peronaea posterior superficialis.

Part II lies between the mm. flexor hallucis longus and tibialis posterior. It corresponds to the whole of embryonic r. communicans inferius.

Part III lies upon the interosseous membrane and gives origin to the rr. communicans and perforans. It is derived from a short persisting section of the embryonic a. interossea.

Part IV passes behind the lateral malleolus to the calcaneus. With the exception of a short section derived from the trunk of the embryonic a. peronaea posterior superficialis, it consists of the r. calcaneus lateralis of that embryonic artery.

In the case reproduced here as fig. 16, the first and second parts of the a. peronaea seem to be normally formed. The fourth part has been taken over by the a. tibialis posterior, while the third part is altogether absent.

In Tiedmann's case, reproduced as fig. 17, the third part of the a. peronaea seems to have been formed by an unusually long r. communicans inferius. The fourth is the only other part of the artery shown; it is of normal composition. The part of the main trunk of the a. peronaea posterior superficialis beyond the origin of its r. calcaneus lateralis, is here represented by a branch of the a. peronaea sufficiently long to clearly indicate its developmental origin.

11. THE PERONAEAL ARTERY IS LARGER THAN USUAL, AND SUPPLIES THE SOLE, THE POSTERIOR TIBIAL BEING PRESENT BUT VERY SMALL. Three examples of this anomaly, differing somewhat in detail, are reproduced as figs. 18, 19 and 20 respectively.

Fig. 18, from Bourgery and Jacob (pl. 50, fig. 2) shows an arrangement of the a. peronaea commonly found in cases of complete absence of the a. tibialis posterior (compare fig. 21). In it the portion of the a. peronaea posterior superficialis beyond the origin of its r. calcaneus lateralis has retained its embryonic connection with the lateral plantar artery. The former vessel can be identified with certainty by its relation to the tendon of the m. flexor hallucis longus. The a. tibialis posterior ends in the supramalleolar region by dividing into a pair of small branches which contribute indirectly to the blood supply of the sole.

Fig. 19, from Tiedmann (pl. 51, fig. 4), represents a case in which the a. tibialis posterior, slender throughout the greater part of its extent, seems to have been reinforced by the embryonic r. coronarius malleolaris above the ankle.

The artery passing distally from the place of reinforcement to the sole follows a course which resembles that of the a. tibialis posterior rather than that of the embryonic a. peronaea posterior superficialis. The absence of any

indication of the positions occupied by the flexor tendons, however, renders the point somewhat doubtful.

In this case the r. coronarius malleolaris seems to have retained its primitive relations, and is continued above the medial malleolus as the a. malleolaris posterior medialis. It is the large branch of communication between the r. coronarius and the a. tibialis posterior which reinforces the latter artery.

An interesting feature of this case is the presence of the persisting proximal end of the embryonic a. interossea, which, arising from the root of the a. tibialis anterior, runs distally posterior to the interosseous membrane. This little vessel, which is frequently present in the adult, marks with certainty the portion of the a. tibialis anterior derived from the embryonic a. poplitea profunda. The a. recurrens tibialis posterior (a remnant of the latter vessel) is not present, unless it is represented by the small medial branch arising from the r. fibularis.

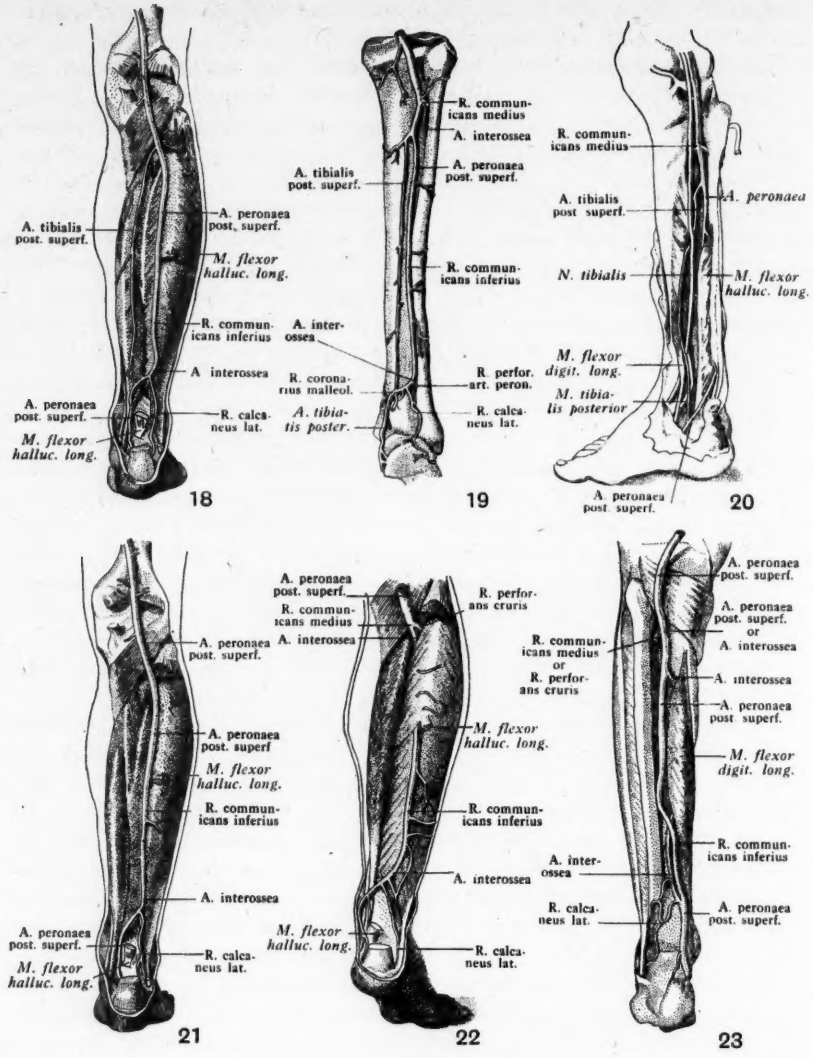
Fig. 20, from Quain (pl. 84, fig. 2), represents an anomaly closely resembling that shown in fig. 18. The distal end of the a. peronaea posterior superficialis has persisted, but joins the small a. tibialis posterior much beyond the point at which the junction has occurred in the case published by Bourgery and Jacob. Whether the trunk formed by the junction of the a. tibialis posterior and the a. peronaea posterior superficialis is to be regarded as a continuation of the former or of the latter artery it seems impossible to determine. The relations of the structures behind the medial malleolus of the original preparation appear to have been purposely disturbed in order to secure a clear reproduction.

In the anomaly reproduced as fig. 19, the a. peronaea retains its normal form. The peronaeal artery in the cases represented in figs. 18 and 20, conforms with the type to which the term "a. peronaea magna" has been given. The composition of the latter vessel is given on p. 138.

12. THE PERONAEAL ARTERY IS LARGER THAN USUAL, AND SUPPLIES THE SOLE, THE POSTERIOR TIBIAL BEING ABSENT: fig. 21, from Bourgery and Jacob (pl. 50, fig. 3). This case has been selected from several published examples of this anomaly. The cases published by Tiedmann (pl. 36, fig. 3), Quain (pl. 84, fig. 3) and Hyrtl (pl. 3, figs. 1 and 2), have not been reproduced here.

All of the cases mentioned above bear a very striking resemblance to one another. The example reproduced differs from all the others in the absence of a small muscular branch which, from its position and direction, seems to represent an imperfect a. tibialis posterior.

In this form of anomaly the a. peronaea, in spite of its great size, is normally constituted except for the fact that the branch which usually arises from the medial side of its fourth part is very large and passes into the sole. The branch which thus connects the a. peronaea with the a. plantaris lateralis takes the form of a continuation of the main trunk of the former artery and represents the persisting distal part of the embryonic a. peronaea posterior superficialis.



Figs. 18–23. In figs. 18, 19 and 20 the posterior tibial artery is small, in 21, 22 and 23 it is absent.

Labels in Roman type refer to the normal embryonic predecessors of the adult arteries shown; italics are used for all other structures. Figs. 18 and 21 from Bourgery and Jacob, pl. 50, figs. 2 and 3 respectively; 19 from Tiedmann, pl. 51, fig. 4; 20 from Quain, pl. 84, fig. 2; 22 from Dubrueil, pl. 17, fig. 1; 23 from Hyrtl, pl. 5, fig. 3.

In Dubrueil's case (fig. 22) the venae comitantes (shown in the original) have been omitted.

The mechanism of the retention of the distal part of the latter artery in cases of absence of the a. tibialis posterior has been reviewed upon p. 140.

The arterial supply of the sole is so frequently effected by means of a modification of the normal a. peronaea that it will be convenient to apply a name to the anomalous vessel which performs this function. It may be called the *a. peronaea magna.*

The a. peronaea magna differs so little, except in size, from the a. peronaea of normal adult anatomy, that a description of the latter artery will apply equally well to the former if the following description of the fourth part be substituted for that given on p. 150:

Part IV. Passes, from a point above and medial to the lateral malleolus, obliquely across the m. flexor hallucis longus, anteriorly to the tendon of which it passes into the sole. Its proximal part gives origin to the r. calcaneus lateralis, which follows the course of the termination of the normal a. peronaea. The fourth part of the artery represents the persisting terminal portion of the embryonic a. peronaea posterior superficialis.

It is unfortunate that none of the cases in which the plantar region is supplied, in the absence of the a. tibialis posterior, by the a. peronaea magna have been posed for reproduction in such a way as to display the distribution of the arteries of the sole. In view of the developmental history of the plantar arteries (reviewed upon p. 163), the absence of the a. plantaris medialis and of the proximal section of the a. plantaris lateralis may be taken for granted.

It is quite possible that in some cases in which the a. tibialis posterior is absent, an artery somewhat resembling the normal a. plantaris medialis may have been produced by unusual elongation of the medial terminal branch of the embryonic a. peronaea posterior superficialis. Something of this nature seems to have occurred in Barkow's case which forms the subject of figs. 24 and 28 of this paper.

Barkow illustrates a sole (*Die Angiologische Sammlung, u.s.w.*, Breslau, 1869, Tab. 9, fig. 2) in which the arterial supply of the area usually occupied by the a. plantaris medialis has been taken over by a supplementary branch of the a. dorsalis pedis. The a. plantaris lateralis in this case is irregular, but the stem from which it arises (labelled a. tibialis posterior) both from its lateral position, and from the fact that it gives origin to typical r. calcaneus lateralis, almost certainly represents a persisting embryonic a. peronaea posterior superficialis.

A case which throws a certain amount of light upon the effect of failure upon the part of the medial terminal branch of the a. peronaea posterior superficialis to join a poorly developed a. tibialis posterior has been reproduced here as fig. 25.

The abnormal composition of the distal portion of the popliteal artery in all cases of anomalous absence of the a. tibialis posterior is referred to under category 5 (p. 138).

13. EMBRYONIC ANTECEDENTS OF THE PERONAEAL PERSIST IN THE FORM OF A SINGLE LARGE ARTERY WHICH SUPPLIES THE SOLE, THE POSTERIOR TIBIAL BEING ABSENT: fig. 22 from Dubrueil (pl. 17, fig. 1). In this case the a. poplitea divides, at the distal border of the m. popliteus, into the a. tibialis anterior and the chief artery of the posterior crural region. The latter at first passes anteriorly to the m. tibialis posterior and then, having pierced that muscle, runs between it and the m. flexor hallucis longus until it turns medially to reach the malleolus.

The portion of the artery beyond the proximal end of the m. flexor hallucis longus corresponds exactly, in embryonic structure, with the second, third and fourth parts of the a. peronaea magna (see pp. 138 and 150). The portion proximal to the point in question, however, differs radically from the first part of that artery.

The course followed by the proximal part of the vessel is not that of the embryonic a. peronaea posterior superficialis but that of the a. interossea. It would seem that, at some stage of development, a branch must have pierced the m. tibialis posterior to effect a connection between the a. interossea and the proximal end of the r. communicans inferius. The alternative blood-channel thus formed would seem to have superseded the collateral section of the a. peronaea posterior superficialis which has been lost.

In such a case as Dubrueil's the composition of the a. poplitea and that of a. tibialis anterior would be involved in the anomaly. The a. tibialis anterior of the case represented in fig. 22 should consist of three parts only, namely, the a. poplitea profunda, the r. perforans cruris and the pars distalis (compare with the composition of the normal artery, p. 141). The part of the a. tibialis anterior derived from the embryonic r. communicans medius is not missing, as in the case represented in fig. 9, but has been added to the distal end of the a. poplitea. This point will be made clear by reference to fig. 4.

14. EMBRYONIC ANTECEDENTS OF THE PERONAEAL PERSIST IN THE FORM OF TWO ARTERIES, ONE OF WHICH SUPPLIES THE SOLE; THE POSTERIOR TIBIAL BEING ABSENT. Two types of anomaly, differing widely in their nature, belong to this category.

Fig. 23, from Hyrtl (pl. 5, fig. 3), represents a case in which the main artery of the posterior crural region gives origin to an aberrant vessel, which rejoins it after having traversed the middle two-fourths of the leg.

It seems impossible, in the absence of the mm. flexor hallucis longus and tibialis posterior, to arrive at a complete determination of the nature of this anomaly. It is probable that the muscles were removed from the original preparation in order to reveal, as fully as possible, the course taken by the arteries. For this purpose also, or by accident, the main artery has been evidently displaced towards the medial side of the leg.

If Hyrtl's figure is not so instructive as it might be, his description is still less so. Employing a criterion which has commonly been used as a basis of interpretation, namely, the relative size of the arteries rather than their

relations to the adjacent structures, Hyrtl merely notes that the a. peronaea follows the medial side of the a. tibialis posterior and rejoins it above the malleolus[1].

Judging from the relations of the vessels the aberrant artery represents a persisting a. interossea. The main arterial trunk is either an a. peronaea magna of normal constitution or one in which the usual first part has been replaced by a component derived from the embryonic a. interossea.

It is the absence of the m. tibialis posterior that prevents the exact determination of the embryonic origin of the part of the main arterial trunk above the aberrant vessel. If this part of the main trunk was originally situated upon the posterior surface of the muscle in question, it would represent the first part of a normally formed a. peronaea magna. If, upon the other hand, it passed anteriorly to the muscle, it would represent a persisting section of the embryonic a. interossea. In the latter case the vessel must have pierced the muscle immediately below the origin of the a. aberrans; the constitution of the main artery of the posterior crural region would be identical with that of the single main occupying the posterior crural region of the preceding case (see fig. 22).

The steps followed in arriving at a conclusion regarding the nature of the aberrant artery and of the part of the main trunk which lies distal to the origin of that vessel, are briefly as follows:

(1) Since there is no embryonic artery which passes between the m. digitorum longus and the tibia, or between that muscle and the m. tibialis posterior, the aberrant artery of this case can be identified as the a. interossea which passes anterior to the latter muscle.

(2) In the formation of the a. peronaea magna the distal end of the part of the a. interossea which becomes the third part of that vessel, ends by joining the part of the a. peronaea posterior superficialis which persists to become the fourth. The origin of the r. calcaneus lateralis from the vessel which, in this case, supplies the sole, forms a sufficient means of identification.

(3) The part of the main vessel, which, in this case, intervenes between the origin and termination of the a. aberrans, ends by joining the a. interossea. It can thus be identified as the r. communicans inferius, which lies between the m. flexor hallucis longus and the m. tibialis posterior and forms the second part of the a. peronaea magna.

The shortness of the part of the a. interossea which, in this case, intervenes between the r. communicans inferius and the distal end of the a. peronaea posterior superficialis and corresponds with the third part of the a. peronaea magna, recalls the relations of the case represented in fig. 17, in which it is absent altogether.

[1] "Streng genommen, fehlte die Arteria peronea nicht. Sie entsprang vielmehr an gewöhnlicher Stelle aus der Tibialis postica. Aber sie bog in der Mitte des Unterschenkels zur Tibialis postica hinüber, lagerte sich an die innere Seite derselben, begleitete sie bis zum inneren Knöchel, und mündete, etwas über diesem, in die Tibialis ein." Hyrtl, *Schlagadern des Unterschenkels*, 1864, p. 265.

Ryan has published a case which must have resembled Hyrtl's very closely, and may even have been a duplicate of it. Ryan's brief description offers no clue as to the nature of the proximal part of the main trunk, which he, like Hyrtl, regarded as the a. tibialis posterior. It leaves no doubt, however, as to the relation borne by the aberrant artery (which he regards as the a. peronaea) to the m. tibialis posterior[1].

Fig. 24, from Barkow (pl. 56, fig. 2), represents a case in which the single arterial trunk of the posterior crural region is the a. peronaea magna. The vessel, however, differs slightly, in its composition, from what may be called the normal type, and gives origin to a large vessel composed of a persisting part of the embryonic a. peronaea posterior superficialis.

The appearance of fig. 24 suggests that the m. flexor hallucis longus has been displaced laterally in order to uncover the distal part of the a. peronaea magna. That this has actually occurred is clearly indicated in fig. 28, which illustrates an earlier stage in the dissection of the same limb.

The peculiar form assumed by the a. peronaea magna in this case appears to have resulted from the unusual position of the connection between the third and fourth parts of that artery.

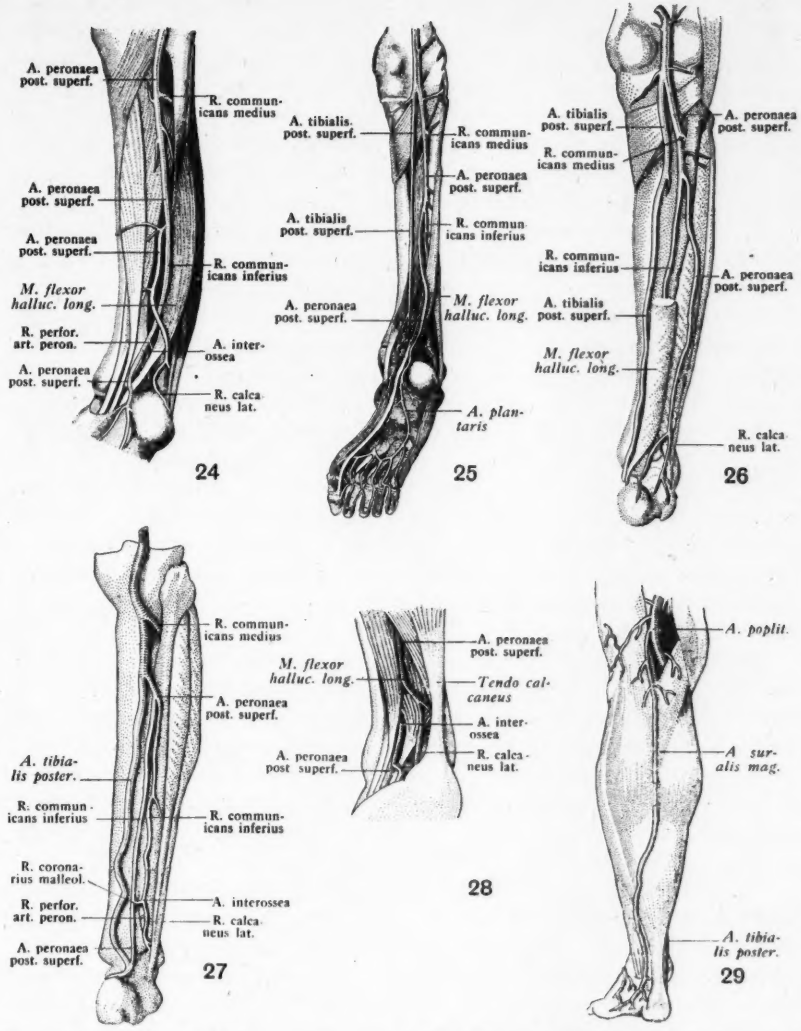
The relations usually borne by the third and fourth parts of the a. peronaea magna to the m. flexor hallucis longus are clearly indicated in figs. 17 and 20. The expectation is that figs. 18, 21, 22 and 23 would have presented a similar picture if the muscle had been retained in the preparations from which they were drawn.

The course of the distal part of the a. peronaea magna shown in figs. 24 and 28 suggests that the connection between the a. interossea and the a. peronaea posterior superficialis occurred near the medial, instead of the lateral, margin of the m. flexor hallucis longus. The connection of the two embryonic vessels in this situation appears to account for the fact that, in Barkow's anomaly, the a. peronaea magna crosses the anterior, instead of the posterior, surface of the m. flexor hallucis longus.

The abnormal persistence of a part of the embryonic a. peronaea posterior superficialis, in the form of a branch of the a. peronaea magna, may also depend upon the site of the connection referred to above. The connecting branch from the a. interossea appears to have joined the a. peronaea superficialis beyond the origin of the r. calcaneus lateralis. The latter branch, although lost to the a. peronaea magna, has been retained by the part of the embryonic a. peronaea posterior superficialis, which has persisted in the form of a branch of the adult artery.

It is interesting to note that Barkow refers to the main artery of the posterior crural region in this case as "the a. tibialis posterior taking the

[1] "Inter arterias maxime irregulares quoad originem et distributionem fibularis enumeranda est....Aliquando superficiei proxima ante tibialem posticam et flexorem pollicis propriam currit, et posticae tibiali conjungitur supra calcem...." Ryan, *Dissertatio inauguralis de quarundam Arteriarum in Corpore Humano Distributione*, 1809, p. 27.



Figs. 24–29. In figs. 24–28 two vessels represent the embryonic predecessors of the peronaeal artery, the posterior tibial being present in all but the first. Fig. 28 shows the correct relations of the arteries of fig. 24 before these were disturbed by further dissection. Fig. 29 is an example of the a. suralis magna.

Labels in Roman type refer to the normal embryonic predecessors of the anomalous adult arteries shown; italics are used for all other structures. Figs. 24, 25 and 28 from Barkow, pl. 56, fig. 2, pl. 8, fig. 2, and pl. 55, fig. 1 respectively; 26, 27 and 29 from Hyrtl, pl. 5, figs. 1 and 2, and pl. 3, fig. 3 respectively.

course of the a. peronaea." Since one or more of the cases in the group belonging to the Breslau collection (see footnote on p. 146) has been described in similar terms, it would seem that this case resembles the supposed examples of absence of the a. peronaea. It may even be one of them.

The a. peronaea magna ends by dividing into the a. plantaris lateralis and a vessel which Barkow labelled as a. plantaris medialis in the original figure. The reason for doubting the correctness of his identification is indicated in the review of developmental history of the plantar arteries given on p. 163.

15. Embryonic antecedents of the a. peronaea persist in the form of two arteries, the posterior tibial being present.

Two types of anomaly have been published which belong to this category. The first type is characterised by the co-existence of the embryonic a. peronaea posterior superficialis and an artery largely composed of the r. communicans inferior. The second type has resulted from the reduplication of the latter vessel.

Fig. 25, from Barkow (pl. 8, fig. 2), and fig. 26, from Hyrtl (pl. 5, fig. 1), are representatives of the first type.

In both these cases the proximal ends of the embryonic aa. peronaea posterior superficialis and tibialis posterior superficialis, by remaining separate, have failed (as in the case represented in fig. 6) to complete the distal end of the a. poplitea. In both cases also the a. peronaea posterior superficialis, which has retained its individuality throughout the leg, gives origin to the a. tibialis anterior.

In Barkow's case of fig. 25, the m. flexor hallucis longus has been displaced laterally for the display of the r. communicans inferius, but not sufficiently to materially alter the primitive relations of the a. peronaea posterior superficialis to that muscle. In Hyrtl's, of fig. 26, the artery has been shifted on to the m. peronaeus longus. In both cases the termination of the r. communicans medius is hidden by the m. flexor hallucis longus, so that it cannot be determined whether it has formed the usual connection with the neighbouring section of the a. interossea or not.

The a. tibialis posterior, which is a much more important vessel in Hyrtl's case than in Barkow's, probably bifurcates normally into the plantar arteries. In the latter case the vessel is extremely small and has failed to produce an a. plantaris medialis or to take over the a. plantaris lateralis in the usual way.

The connection shown in fig. 25 between the termination of the a. peronaea posterior superficialis and the a. plantaris lateralis is quite in accordance with the views I have already expressed.

Fig. 27, from Hyrtl (pl. 5, fig. 2), differs from the two preceding cases in that both the arteries in the peronaeal region lie deep to the m. flexor hallucis longus. Although the muscle is not represented in the figure, Hyrtl makes a perfectly clear statement regarding this point: "Die beiden peronaeae sind dann profundae, und liegen im canalis musculo-peroneus hart nebeneinander."

Since the proximal parts of the two arteries of the peronaeal region occupy the position normally held by the second part of the a. peronaea, it is difficult to escape the conclusion that they have resulted from a reduplication of the embryonic vessel from which that artery arises, namely, the r. communicans inferius.

The distal part of the more lateral of the two arteries gives origin to the r. communicans and r. perforans and ends as the r. calcaneus lateralis. It seems, therefore, to have been derived from the embryonic precursors of the third and fourth parts of the a. peronaea (see p. 150).

The origin of the distal part of the more medial of the two trunks can scarcely be determined with certainty in the absence of any indication of its relation to the tendon of the m. flexor hallucis longus. Comparison with fig. 26, however, suggests the probability of its derivation from the terminal part of the main trunk of the a. peronaea posterior superficialis.

The short stem of the double artery, since it arises from the a. tibialis posterior at the usual site of origin of the a. peronaea, probably represents the first part of that vessel. It is to be presumed, therefore, that it rests upon the posterior surface of the m. tibialis posterior and represents a persisting section of the a. peronaea posterior superficialis.

Green has described and figured an example of so-called double a. tibialis posterior (*An Account of the Varieties of the Arterial System*, Dublin, 1820, pl. 6, fig. 1) which very probably represents an example of one of the two types of anomaly under consideration. His exceedingly diagrammatic figure indicates the contour of the leg and shows the a. poplitea giving off three branches which course longitudinally through the posterior crural region. From the absence of any indication of the relations of the arteries it is impossible to form an opinion as to the essential nature of the case. The evidence, however, afforded by the study of development and of figures of kindred anomalies does not favour the acceptance of Green's interpretation.

16. A. SURALIS MAGNA: fig. 29, from Hyrtl (pl. 3, fig. 3), represents a case in which a large artery accompanies the v. saphena parva through the leg to the dorsal aspect of the foot. An almost identical case has been figured by Oesterreicher (*Anatomischer Atlas oder bildliche Darstellung des menschlichen Körpers neu bearbeitet von M. Erdl*, München, 1845, pl. 93, fig. 2). Another case in which the distribution of the artery is not so extensive has been published by Haller (*Icones Anatomicae*, Fasic. 8, pl. 2).

The a. suralis magna, which occurs occasionally in the adult limb, can scarcely be regarded as having resulted from the persistence of a normal embryonic vessel, for its presence in the embryo has not yet been recorded. The artery, no doubt, arises during the development of the limb, but it must occur almost as rarely in the embryo as in the adult.

The fact that the a. suralis magna has taken origin from the a. poplitea in all the cases hitherto published as examples of this anomaly, would lead, rather naturally, to the supposition that the appearance of this anomalous

vessel had depended upon the excessive development of one of the a. surales superficiales. Such a supposition may eventually prove to be well founded, but a review of the conditions associated with the appearance of other anomalous arteries cannot be regarded as supporting it.

The occurrence of supernumerary arteries in the adult lower limb depends usually upon the anomalous persistence of embryonic channels which normally disappear during the later stages of development. The case of the a. saphena magna, however, forms an exception to the general rule. The occasional appearance of this artery in the adult may perhaps be taken as the manifestation of a tendency towards excessive growth which might be inherent in a terminal branch of such a rapidly growing artery as the embryonic a. femoralis. No anomalous artery has yet been recorded which appears to owe its existence to the fortuitous enlargement of a minor offshoot of one of the regular vessels of the lower limb.

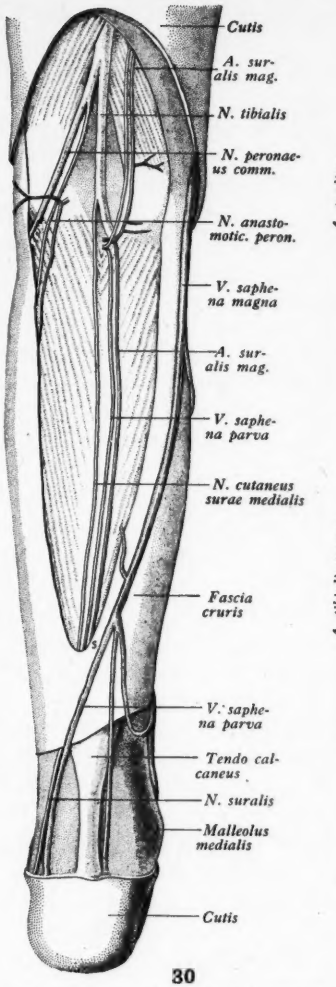
Barkow has published a figure which suggests the possibility that the a. suralis magna may not arise in the first place from the a. poplitea at all, but that it may have been taken over by that vessel by means of a secondary anastomosis. Barkow's figure was primarily intended to record an anomaly affecting the v. saphena parva. The connections of the small artery which accompanies this vein and its continuation through the leg and thigh, probably on that account, are not fully displayed. The figure however taken in conjunction with the embryological possibilities, if not entirely conclusive, may be regarded as extremely suggestive.

Fig. 30, from Barkow (pl. 57, fig. 1), represents a left leg in which the distal part of the v. saphena parva is drained, above the malleoli by a tributary of the v. saphena magna. Following the course usually taken by the v. saphena parva upon the back of the leg is a small vein which communicates with the v. poplitea behind the knee. Above the knee the vein pursues a course which identifies it as the further continuation of the embryonic v. ischiadica.

Traversing the leg upon the medial side of the small v. saphena parva, is a slender artery, which, according to the author's explanation, terminates below, at the point marked *S*, deep to the fascia. The artery appears to arise from a branch of the a. poplitea to the gastrocnemius muscle, and is unquestionably an imperfect example of the a. suralis magna. Extending upwards from the apparent origin of vessel is a small artery which can be traced through the lower part of the thigh to the point at which it disappears beneath the fascia lata. Barkow gives no information whatever regarding the latter part of the artery. It is quite possible, however, that it may represent a prolongation of the a. glutaea inferior.

The possibility just referred to is suggested by the nature of the changes undergone by the more proximal of the two parts into which the a. ischiadica divides when its original continuity has suffered interruption.

At the stage of 18 mm. the a. ischiadica is a continuous vessel which, following the course of the n. tibialis through the thigh, gives origin to no extra-



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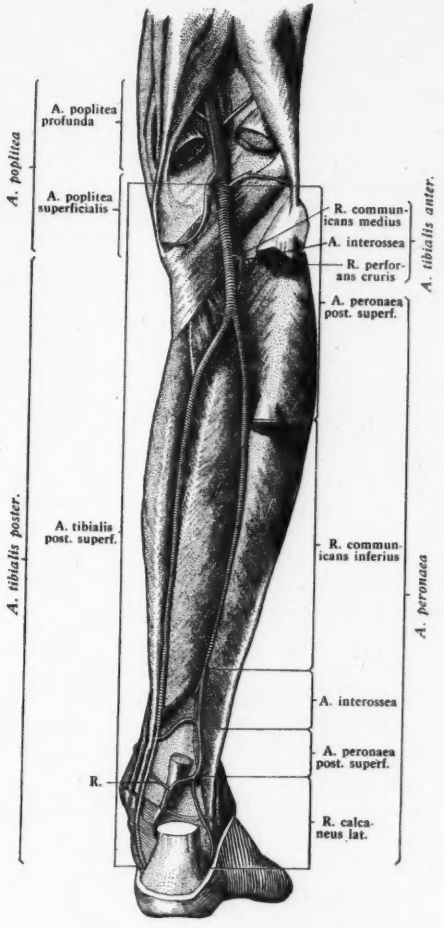

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Fig. 30 represents a superficial dissection of the left leg copied, with negligible modification, from Barkow's pl. 57, fig. 1.

The case was originally published to record an anomaly of the v. saphena parva, but is reproduced for the sake of the light it appears to throw upon the origin of the a. suralis magna.

Fig. 31 represents a right leg from which the superficial calf muscles, and the flexor hallucis longus have been removed to show the normal distribution of the arteries of the popliteal and posterior crural regions.

The main arteries of the adult are labelled in terms of the embryonic vessels which enter into their composition; italics being used for the names of the adult, and Roman type for the embryonic vessels. The adult arteries representing persisting portions of the primitive axial artery are coloured red.

pelvic branches. At the stage of 22 mm. the continuity of the artery has been broken near the site of origin of the n. tibialis from the lumbo-sacral plexus. The distal portion of the vessel has become engaged in the formation of an extensive anastomosis upon the posterior aspect of the m. adductor magnus. The extremity of the proximal portion of the a. ischiadica has left the position formerly occupied by the original vessel upon the n. tibialis to accompany the n. femoris cutaneus posterior and the v. ischiadica to the surface of the limb.

The proximal part of the a. ischiadica persists in adult life as the a. glutaea inferior. Its termination, no doubt, normally furnishes the muscular and cutaneous branches of the lower glutaeal region.

The fact that the a. glutaea inferior follows the embryonic v. ischiadica for a short distance in the upper part of the thigh would seem to give but slight support to the theory that it may occasionally follow it as far as the foot. Barkow's figure, however, suggests that this may be the case, in spite of the fact that the continuity between the artery upon the back of the thigh has not been demonstrated.

If the artery which, in Barkow's case, follows the v. ischiadica, should have proved, upon examination, to be continuous with the a. glutaea inferior, the evidence would have been conclusive. It would have been scarcely less so if the artery had ended blindly upon the posterior surface of the thigh. In the event of the artery in question having been found to join one of the aa. perforantes the evidence would have been merely negative.

An a. glutaea magna long enough to extend throughout the length of the limb (in the event of an undoubted example of this anomaly being found) might well be regarded as forming a common basis of the two variants of the a. suralis magna which have been published. A long and probably slender artery of this character would almost certainly communicate with the a. poplitea behind the knee. Such an anastomosis would not be unlikely to lead to the secondary degeneration of the proximal part of the artery; it might produce, in fact, a condition similar to that shown in fig. 29.

It is extremely probable that the shortening of the a. saphena magna, indicated in fig. 15, has been accomplished through the agency of a secondary anastomosis similar to that which might have produced the shortening of the a. suralis magna. It is not unlikely, also, that the condition of the arteries of the anterior crural region shown in fig. 12 has resulted from the partial suppression of an originally complete a. tibialis anterior depending upon a secondary anastomosis between that artery and the a. tibialis posterior.

The identity of the a. suralis magna and the a. glutaea inferior cannot, by any means, be regarded as definitely established. The publication of cases throwing light upon the origin of the vessel known as the a. suralis magna, or as the a. saphena parva, is very much to be desired.

D. THE FOOT

The main arterial channel of the foot consists of a continuous loop of which the component parts are known, in adult anatomy, as the a. plantaris lateralis, the arcus plantaris, the r. plantaris profundus and the a. dorsalis pedis. From an embryological standpoint, however, it is convenient to divide the loop into two parts only. One of these consists of the a. plantaris lateralis, while the other embraces the part formed from the three remaining vessels.

The embryological distinction is based upon the fact that the a. plantaris lateralis is derived from the terminal bifurcation of an artery of the leg, namely, the a. peronaea posterior superficialis, while the other part of the loop arises from the embryonic arterial retia of the foot.

During the earlier period of development the plantar and dorsal arterial retia of the foot retain their primitive form and communicate with one another around the borders of the foot and between the digits. The plantar rete receives its blood from the a. interossea and the dorsal through the r. perforans tarsi.

At the stage of 18 mm. the appearance of the arterial retia has been modified by the development of three new arterial channels in the leg which have extended into the foot.

The three arterial channels in question are the a. tibialis posterior superficialis, the a. peronaea posterior superficialis and the a. tibialis anterior, pars distalis. Soon after these vessels have formed their definitive connections, the distal part of the a. interossea and its perforating tarsal branch undergo degeneration.

The distal ends of the arteries extending from the leg into the foot are disposed in the following way:

The terminal part of the a. tibialis posterior superficialis extends along the medial side of the sole, but is very slightly connected with the rete plantare. It becomes the *a. plantaris medialis.*

The a. peronaea posterior superficialis bifurcates, upon entering the sole, into medial and lateral terminal branches. The medial branch joins the a. tibialis posterior superficialis and thus marks the point at which the adult a. tibialis posterior bifurcates into the aa. plantares. The lateral branch crosses the developing muscles of the sole to join the rete plantare near the base of the fifth metatarsal. The medial and lateral branches together form a direct channel which becomes the *a. plantaris lateralis.*

The a. tibialis anterior, pars distalis, ends by joining the rete dorsale in front of the ankle joint.

The consequence of the alteration in the site at which the retia of the foot receive the entering blood-stream is clearly to be distinguished at the stage of 22 mm. At that period of development a very definite main arterial track is outlined by the enlargement of the elements of the original retia which intervene between the termination of the a. plantaris lateralis and that of

a. tibialis anterior. The course taken by the track in question marks it as forming the part of the main arterial loop of the adult foot which is formed by the *arcus plantaris*, the *r. plantaris profundus* and the *a. dorsalis pedis*.

As already pointed out, absence of the a. plantaris medialis results from the absence, or imperfect development, of the embryonic a. tibialis posterior superficialis. It is associated with absence of the medial section of the a. plantaris lateralis and with the supply of the sole by the a. peronaea magna or an artery of kindred embryonic antecedents. Fig. 25 is an example of this form of anomaly.

With the exception of the anomaly just mentioned and of Hyrtl's unique case of persistence of the r. perforans tarsi, the more important anomalies of the foot may be divided into two general categories. The first of these comprises the recorded examples of absence of one or more of the elements of the arterial loop of the foot which have been derived from the embryonic retia. The second comprises the cases in which the loop, although fully formed, is characterised by a more or less localised irregularity of calibre.

17. Examples of incomplete loop: fig. 32, from Hyrtl (pl. 10, fig. 1), represents a case in which the distal end of the a. tibialis anterior breaks up into an arterial plexus which has probably preserved the main features of the embryonic rete dorsale. Apart from the aa. metatarsae dorsales none of the arteries usually found upon the dorsum of the foot are recognisable. Hyrtl states that the rr. perforantes are lacking but gives no information regarding the arterial supply of the sole.

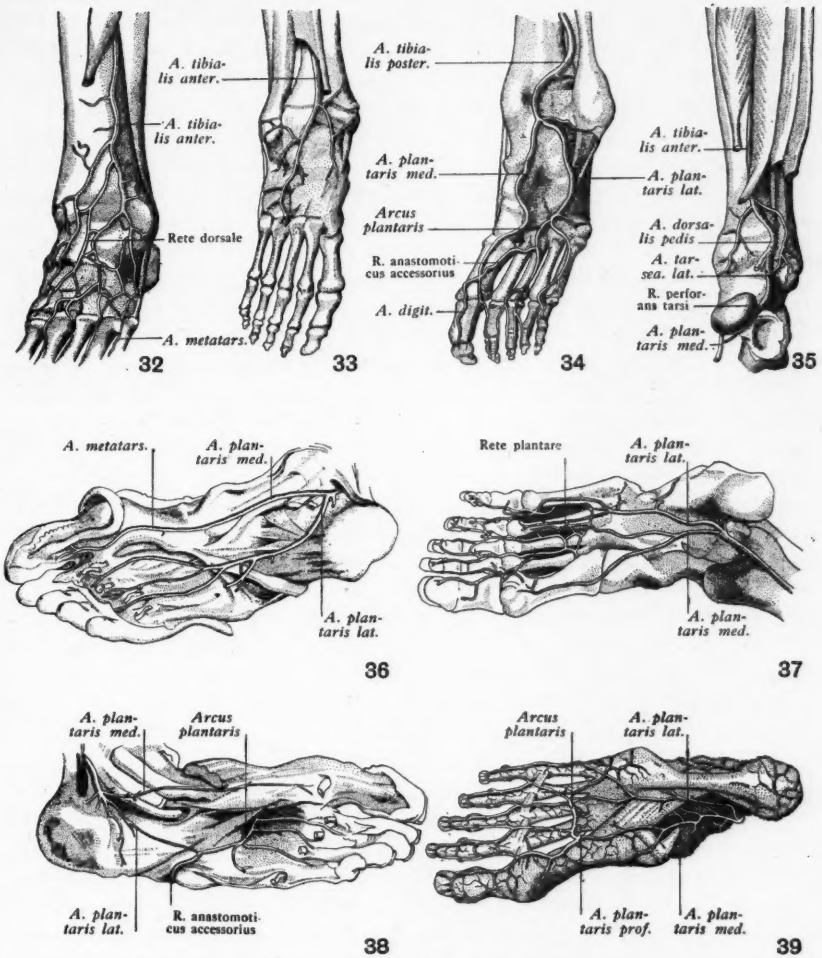
Figs. 33 and 34, from Hyrtl (pl. 9, figs. 1 and 2 respectively), represent the dorsal and plantar surfaces of the same right foot. The a. dorsalis pedis is incomplete, and the r. plantaris profundus absent; there are no aa. metatarsae dorsales. In the sole, the arcus plantaris, which is small and irregular, is completed by a connection between the first and second plantar metatarsal arteries. The a. plantaris medialis is unusually large and ends as the first plantar metatarsal artery.

Fig. 36, from Quain (pl. 86, fig. 4), represents a sole which, in its arterial distribution, somewhat resembles the case represented in fig. 34. The arcus plantaris ends, however, as the second plantar metatarsal artery, and does not join the first plantar metatarsal which forms the termination of the large a. plantaris medialis.

In all the cases cited above, the absent section of the arterial loop of the foot belongs to the part derived from the embryonic retia. Absence of the part of the loop formed by the a. plantaris lateralis, which is derived from the embryonic a. peronaea posterior superficialis, has not been recorded.

The site of the initial departure from the normal course of arterial development upon which the production of anomalies of this class depends is difficult to localise. Figs. 32, 33, 34 and 36 would seem to favour its localisation in retia of the foot.

18. Examples of irregular loop. Fig. 37, from Barkow (pl. 10, fig. 4),



Figs. 32–39. The arterial loop of the foot is incomplete in figs. 32, 33, 34 and 37, irregular in 38 and 39. Fig. 35 is an example of persistence of the r. perforans tarsi.

Labels in Roman type refer to the normal embryonic predecessors of the anomalous adult arteries shown; italics are used for all other structures. Figs. 32–35 from Hyrtl, pl. 10, fig. 1; pl. 9, figs. 1 and 2, and pl. 10, fig. 3 respectively; 36 and 38 from Quain, pl. 86, figs. 4 and 5 respectively; 37 from Barkow, pl. 10, fig. 4; 39 from Tiedmann, pl. 37, fig. 6.

represents a case in which the arcus plantaris has been replaced by an arterial plexus which probably represents a partial survival of the embryonic rete plantare. Blood enters the plexus through the ordinary channels, namely the r. plantaris profundus and the a. plantaris lateralis. There is an additional connection between the a. plantaris medialis and the plexus by means of a branch which probably has arisen also from the embryonic rete.

Figs. 38 and 39, from Quain (pl. 86, fig. 5), and Tiedmann (pl. 37, fig. 6), respectively represent cases in which the a. plantaris lateralis is unusually small. The arcus plantaris appears to be of normal size in both examples, although, in Tiedmann's, the lateral end of the arcus has been replaced by what appears to be a survival of the embryonic rete plantare.

The maintenance of the calibre of the arcus plantaris is due, in Quain's case, to reinforcement of blood-flow through a branch (probably a lateral tarsal) arising upon the dorsum of the foot. In Tiedmann's anomaly, compensation has been established by the r. plantaris profundus and by a branch of the unusually large a. plantaris medialis. In the former case the disturbance of calibre is localised to the part of the loop formed by the a. plantaris lateralis, while in the latter, the size relations have been disturbed throughout a much more extensive section of the loop.

The anomalies cited in the literature as consisting in the smallness of one or other of the vessels entering into the composition of the arterial loop of the foot are not actually confined to the vessels most obviously concerned. The compensatory enlargement which occurs in other parts of the loop, or in a neighbouring vessel, is also a part of the anomaly.

The production of anomalies of this class seems to depend rather more frequently upon irregularities affecting the development of the arteries passing from the leg to the foot than upon developmental irregularities of the retia themselves. While figs. 38 and 39 suggest the former conclusion, the conditions shown in fig. 37 would seem to show that it is not of universal application. That the size of the a. dorsalis pedis is not necessarily dependent upon the condition of the distal end of the a. tibialis anterior is shown by figs. 12 and 13.

An interesting class of minor anomaly of the a. dorsalis pedis is that afforded by modification of the usual course of this artery in cases in which the a. perforans arteriae peronaea is not of unusual magnitude. The a. dorsalis pedis, instead of pursuing its usual direct course, exhibits a lateral convexity which brings the distal end of the artery into a line between the interior end of the tibio-fibular interval and the first inter-metatarsal interspace. Such cases suggest that the a. perforans arteriae peronaeae may have maintained a temporary ascendency over the distal part of the a. tibialis anterior during a sufficiently long period of development to have impressed an unusual direction upon the course of the a. dorsalis pedis. Cases in which a less obviously indirect a. dorsalis pedis passes immediately over the dorsal end of the sinus tarsi suggest in a like manner that the r. perforans tarsi may

have been unusually tardy in yielding its area of supply to the later developed a. tibialis anterior.

19. Persistence of the r. perforans tarsi. Fig. 35, from Hyrtl (pl. 9, fig. 3), represents a case in which an artery of considerable size, derived from the embryonic r. perforans tarsi, occupies the tarsal sinus.

A minute artery, of which the connections are similar to those shown in Hyrtl's figure, is not infrequently to be found traversing the sinus of a well-injected subject. No case, however, seems to have been published of which the importance approaches that of Hyrtl's.

In this case the artery is described as a branch of the a. dorsalis pedis which, arising from the lateral side of the parent vessel, traverses the tarsal sinus to join the a. plantaris medialis. In accordance with the description, the figure suggests that the blood-stream through the anomalous vessel takes a direction contrary to that which it follows in the embryo.

The vessel of Hyrtl's case appears to be of composite origin. Its plantar end is derived from a portion of the embryonic rete plantare which, possibly combined with an element derived from the a. interossea, has formed a permanent connection with the a. plantaris medialis. The dorsal end is a derivative of the rete dorsale which might otherwise have become an ordinary a. tarsea lateralis. The extent and connections of the vessel have been admirably shown by the removal of the anterior part of the foot after the manner of Chopart's amputation.

Cases in which the circulation of the foot is modified by the presence of the a. saphena magna and a. suralis magna have already been noted.

THE RELATION OF EACH OF THE EMBRYONIC ARTERIES TO THE FORM ASSUMED BY THE ARTERIAL SYSTEM OF THE ADULT LEG AND FOOT

A. interossea. A short section of this artery persists as the third part of the normal a. peronaea. A similar section becomes the third part of the single anomalous artery of the posterior crural region known as the a. peronaea magna (figs. 18, 21 and 24), and as the corresponding part of the main artery of that region shown in figs. 22 and 23.

The section of the a. interossea in question has contributed little to the formation of the a. peronaea magna, of fig. 23, and nothing to the a. peronaea of figs. 17 and 18. In the last case it persists but has formed abnormal connections.

The a. interossea has persisted in the upper third, and in the middle two-fourths of the leg respectively, in the cases reproduced as figs. 22 and 23.

A small piece of the proximal end of the a. interossea not infrequently persists in the adult as an insignificant branch of the second part of the a. tibialis anterior. This branch usually arises near, or in common with, the origin of the r. fibularis, and runs downwards in contact with the posterior

surface of the membrana interossea. An example of its persistence is recorded in fig. 19.

A. ischiadica. Two sections of this artery are present in the normal adult. The more proximal of these becomes the a. glutaea inferior, while the more distal is transformed into the post-femoral anastomosis.

Anastomosis between a persisting part of the a. ischiadica and the adult a. poplitea is illustrated in figs. 10 and 11. Whether the a. suralis magna (see figs. 29 and 30) should be regarded as representing an abnormally large a. glutaea inferior is an open question.

A. peronaea posterior superficialis. Two parts of this artery persist in the normal adult, also its two terminal branches. The proximal portion of the vessel participates in the formation of the distal part of the a. poplitea and the proximal part of the a. tibialis posterior. A more distal section becomes the first part of the a. peronaea. A still more distal section persists, in combination with the r. calcaneus lateralis which arises from it, as the fourth part of the same artery. The medial and lateral terminal branches become the proximal and distal parts, respectively, of the a. plantaris lateralis.

The entire a. peronaea posterior superficialis has persisted, together with its lateral terminal branch, in the case represented in fig. 25; the main stem is present also in the case shown as fig. 26. In the latter case it is likely that the terminal branches have participated normally in the production of the a. plantaris lateralis.

The proximal part of the a. peronaea posterior superficialis has formed the distal part of the a. poplitea without the participation of the embryonic a. tibialis posterior superficialis in the cases reproduced in figs. 21, 22, 23 and 24.

The entire failure of the proximal part of the a. peronaea posterior superficialis to blend with the adjacent section of the a. tibialis posterior superficialis of the cases represented as figs. 6, 25 and 26 has led to anomalies of the aa. poplitea, tibialis posterior and peronaea. The partial failure shown in figs. 7 and 8 has resulted in anomalies of the aa. tibialis posterior and peronaea, and in the latter case, of the aa. poplitea and tibialis anterior also.

A portion of the a. peronaea posterior superficialis which normally disappears in the course of development has been retained as a branch of the a. peronaea magna of fig. 24. It appears, also, as a branch of the right a. peronaea of the case represented in Haller's fasciculus 8, pl. 2, which is not reproduced here.

The distal end of this artery has persisted in the form of the fourth part of the a. peronaea magna of figs. 18, 20, 21 and 24, and as the corresponding part of the chief artery of the posterior crural region of figs. 22, 23 and 25.

A. poplitea profunda. The proximal portion of this artery invariably persists to become the part of the adult a. poplitea which extends from the hiatus tendineus to the origin of the a. genu inferior medialis. Its distal portion is represented by the root of the a. genu inferior medialis, by the

second part of the a. tibialis anterior and by the entire a. recurrens tibialis posterior of the normal adult.

Persistence of the entire distal portion of the a. poplitea profunda, in the form of the first part of an abnormal a. tibialis anterior, is shown in fig. 9. Persistence of this portion of the vessel as the distal part of the adult a. poplitea occurs normally in many mammals.

The nature of the connections of the proximal part of the a. poplitea shown in figs. 10, 29 and 30, respectively, have been noticed above (see a. ischiadica).

A. poplitea superficialis. This artery, formed by the union of the proximal parts of the aa. tibialis posterior superficialis and peronaea posterior superficialis, normally becomes the distal part of the adult a. poplitea.

The part of the a. poplitea derived from this vessel is of normal composition, though small, in the case represented in fig. 9. Its composition in the cases shown in figs. 21, 22, 23 and 24, and the cause of its absence in figs. 6, 25 and 26, are noted above (see a. peronaea posterior superficialis).

The a. poplitea superficialis was probably derived mainly from the a. peronaea posterior superficialis in the cases reproduced as figs. 18, 19 and 20. The significance of the connection between the persisting part of the a. ischiadica and the distal part of the a. poplitea of fig. 11 is suggested above (see a. ischiadica).

A. tibialis anterior, pars distalis. In normal development this artery becomes the fourth part of the adult a. tibialis anterior. Its imperfect development is illustrated by fig. 13. Its absence, probably secondary, is shown in fig. 12.

A. tibialis posterior superficialis. This artery persists in adult life in its entirety. The proximal portion normally participates, with the a. peronaea posterior superficialis, in the formation of the distal part of the adult a. poplitea and of the proximal part of the a. tibialis posterior. A more distal portion becomes the part of the latter artery which lies beyond the origin of the a. peronaea. The most distal part of all becomes the a. plantaris medialis.

The absence of this artery in the cases reproduced in figs. 21, 22, 23 and 24, has led to the absence of the adult a. tibialis posterior. The effect of its absence upon the composition of the a. poplitea has already been noted (see a. peronaea posterior superficialis). The probable effect of absence of the a. tibialis posterior upon the form of the aa. plantares has been discussed upon p. 164. Imperfect development of this artery probably lies at the root of the anomalies of the a. tibialis posterior and a. peronaea shown in figs. 18, 19 and 20.

The effect of the complete failure upon the part of the a. tibialis posterior superficialis to unite with the corresponding section of the a. peronaea posterior superficialis, shown in figs. 7 and 8, has been referred to above (see a. peronaea posterior superficialis).

The peculiar form of the a. tibialis anterior in the case reproduced as fig. 12,

and that of the a. saphena magna in the case of fig. 15, appears to depend upon the formation of unusual anastomoses by the a. tibialis posterior superficialis. The normal communication (*R*) between the a. tibialis posterior superficialis and the a. peronaea posterior superficialis is responsible for the fourth part of the a. peronaea having become a branch of the a. tibialis posterior in the case represented in fig. 16.

R. calcaneus lateralis. This branch of the a. peronaea posterior superficialis persists to form the larger portion of the fourth part of the a. peronaea, and is represented by the termination of that adult artery.

It appears as a branch of the fourth part of the a. peronaea magna in figs. 18 and 21, and of the chief artery of the posterior crural region in figs. 22 and 23. It appears also as a branch of the persisting a. peronaea posterior superficialis of fig. 26, and of the lateral element of the double a. peronaea of fig. 27. In the case represented in fig. 24, it appears as the termination of a large branch of the a. peronaea, and in that reproduced as fig. 16, as a branch of the a. tibialis posterior.

R. communicans inferius. In normal development this branch becomes the second part of the adult a. peronaea. In the case represented as fig. 17 it seems to have formed the third part also.

In the cases reproduced as fig. 22 it follows upon a persisting section of the a. interossea in the formation of the chief artery of the posterior crural region. It is reduplicated in the case forming the subject of fig. 27.

R. communicans medius. This branch becomes the first part of the normal a. tibialis anterior.

It is absent in the case represented by fig. 9, forms the second part of the abnormal a. tibialis anterior of fig. 8, and enters into the composition of the abnormal a. poplitea of fig. 22.

R. coronarius malleolaris. This branch of the a. interossea normally persists in the adult leg as the r. communicans and as the aa. malleolares posterior et anterior mediales.

In the case reproduced as fig. 19 it reinforces the distal part of the a. tibialis posterior.

R. perforans cruris. This branch of the a. poplitea profunda forms the third part of the normal a. tibialis anterior of the adult.

The r. perforans cruris seems to have failed to fulfil its usual function in Velpeau's case discussed on p. 141. There are no graphic records of anomalies which depend upon the abnormal disposition of this branch, or upon its absence.

R. perforans tarsi. This terminal branch of the a. interossea disappears during the course of normal development. Fig. 35 records an example of its persistence.

R. saphenus. This, the medial terminal branch of the embryonic a. femoralis, persists as the a. genu suprema and as the r. saphenus of that vessel.

Examples of abnormal overgrowth of this branch to form a vessel known

as the a. saphena magna are recorded as figs. 14 and 15. The origin of this artery from the a. tibialis posterior, in the latter case, is the result of a secondarily acquired anastomosis.

The arterial retia of the embryonic foot give rise, in normal development, to the arcus plantaris, to the aa. dorsalis pedis, arcuata, tarseae, metatarseae and digitales and to the rr. plantaris profundus and perforantes.

Abnormal development of the embryonic *retia pedis* is exemplified as follows:

In figs. 34, 36 and 39 the arcus plantaris is defective, in fig. 37 it is absent. Figs. 32 and 33 illustrate absence of the a. dorsalis pedis and of the a. arcuata. In the case represented in fig. 33, the aa. metatarsales et digitales dorsales are absent; so also is the r. plantaris profundus of the cases shown in fig. 32, in figs. 33 and 34, and in fig. 36. The rr. perforantes are absent in the cases represented in fig. 12 and in figs. 33 and 34.

THE MATURATION OF THE HUMAN OVUM[1]

By ARTHUR THOMSON

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The Human Anatomist is handicapped by the nature of the material with which he has to deal. More particularly is this the case when the problem attacked involves the recognition of delicate changes in cellular structure. It is only exceptionally, as in operation cases, that he can get his tissues fresh. Under ordinary circumstances a considerable period must have elapsed, amounting in some cases to days, before the organ or tissue desired can be obtained post-mortem.

Further, the time and manner of death may exercise important influences on the condition of the parts to be examined, for it will be obvious that if death occur during the warm summer months the putrefactive changes that ensue will be more rapid than those occurring in a cold season. Similarly the processes involved in death after prolonged illness are likely to produce changes in the tissues of an abnormal kind, differing in this respect from those met with in sudden death either by accident or acute disease.

From all, or most of these conditions, the zoologist is happily free. Engaged in a like or similar enquiry, he can kill the animal selected whilst still in a normal condition, and thus obtain its tissues and organs fresh. Subjected alike to similar processes of fixation and staining, the results obtained from these two different sources of supply, human, as distinct from animal, must necessarily vary in the refinement and delicacy of the appearances observed though what the resulting differences may be when comparing the "fresh" with the "stale" tissue, is still a matter of doubt.

In such an enquiry as that here involved, we must be content with what we can get. In the present instance the specimens examined have all been obtained from women who died suddenly or were accidentally killed, but the necessary delay incurred in obtaining and performing a post-mortem examination must militate against the freshness of the material examined. Of the possible changes that may intervene during the period of death and fixation we are ignorant, and whilst admitting that some such changes may affect the more delicate structures involved, such as the fibrillar appearance of the asters and the arrangement of the chromosomes, there is sufficient evidence to justify us in assuming that the grosser phenomena involved in the division of the egg, such as the position of the nucleus, the presence or absence of a nuclear membrane, the occurrence of centrospheres and the presence of polar

[1] The expenses of illustrating this paper were defrayed by the Medical Research Committee.

bodies can all be identified, though possibly in a form differing somewhat from those met with in the fresher material.

The utmost care has been exercised in the fixing, cutting, mounting and staining of the tissues examined. Where possible complete serial sections of the eggs examined have been reproduced, on a reduced scale, so that in the plates provided a complete conspectus of the contents of the egg is available.

Thanks to the great industry and skill of my Laboratory Assistant, Mr W. Chesterman, to whose ability and enthusiasm I am greatly indebted, the sections obtained are as good as the conditions permit.

A word or two as to the method of illustration adopted. As the result of our united efforts, Mr Chesterman has acquired a high degree of skill in the production of photomicrographs, these I have utilised without exception in the present paper, for, though laying claim to some experience as a draughtsman, I have come to the conclusion that well executed microphotographs are of much more value than elaborately executed drawings; in the latter the draughtsman is unwittingly led to emphasise those details which he thinks of importance, whilst at the same time he may omit features which for the time being he considers of little moment. In numerous instances a structure which at first appeared of no account has been found subsequently to form a link in the chain of evidence.

The production of such microphotographs is tedious and tiresome, and demands an intimate knowledge of the technique required, but the results, in my opinion, justify the amount of labour and expense involved. In the present instance the illustrations may be relied upon as affording an accurate record of the appearances described. They are a record of the facts, the reader may deduce from them such conclusions as he thinks justifiable—I ask no more.

In work of this kind, where delicate measurements are involved, I have departed somewhat from the approved method, as I found it so irksome and in some instances so difficult of application—I mean the use of the eyepiece micrometer in conjunction with a stage micrometer. What has been done in every case where a photomicrograph was taken was to introduce at the same time and under similar conditions of the optical arrangement a stage micrometer, so that the degree of magnification could be accurately gauged on the ground glass of the camera. In this way the amplification of the image on the positive or negative photograph was accurately known, and by a simple calculation in reduction, the magnification being known, the precise measurements of the various details exhibited in the sections were readily deduced from their measurement on the print.

In regard to the present enquiry—the maturation stages of the human egg—no observations, so far as I know, have yet been published. It may be that like or similar appearances have been seen, but hitherto no attempt has been made to arrange them in their order of sequence.

Our conception of what occurs in the human female has hitherto been based on our knowledge of what takes place in lower forms. So extensive is

the literature of that subject that no reference need here be made to it, other than to accept the general conclusions based upon it as set forth in the various text-books on Human Anatomy, in which a general description of the changes presumably involved, is set forth. It is assumed that the reader is familiar with one or other of these accounts, and consequently space has been economised by taking such information for granted. It may be stated broadly that the results obtained conform to the general plan of the descriptions given as applicable to the mammalian type, the only point of difference, as will

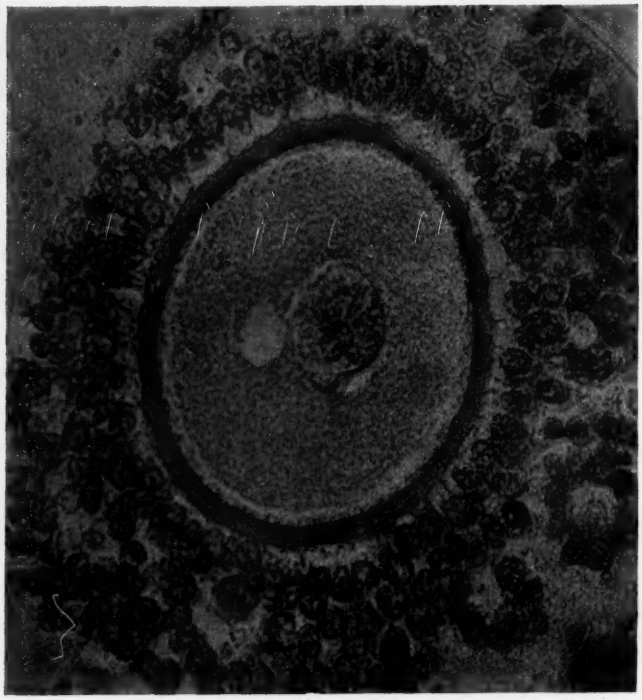

FIG. 1. Human ovum in discus proligerus in early part of prophase of first division. ×600.

be subsequently explained, depending on the solution of the question as to whether or no the oocyte in man is mature, i.e. has passed through the stages of its first and second division, before it leaves the ovary. It appears on the authority of numerous observers that this is not the rule in Vertebrates, and that the sperm enters the ovum during the stage of the second maturation division. If this be so, it will appear on the evidence adduced that man is an exception to the rule. The details, however, on which this and other conclusions are based, had better be postponed until the eggs have been fully examined. We will therefore proceed forthwith with their description.

Here let me say how much I am indebted to my friends holding pathological appointments for their ever ready help in providing me with suitable material.

The first figure is that of a section, 0·007 mm. thick, stained with Mallory's Connective Tissue Stain, of an ovum in the discus proligerus of a Graafian follicle from a woman aged 22 who died from a femoral hernia.

The egg including the Zona pellucida measures 0·1 × 0·09 mm., measured from the inner surface of the Zona pellucida its diameters are 0·097 × 0·08 mm.

It will be obvious from the figure and from the measures given that the egg is not a sphere as so frequently described but as will be seen later exhibits an oval form.

The cells of the Corona radiata are adherent to the external surface of the Zona pellucida by slender filaments with *spaces between.*

The structure of the Zona pellucida is not homogeneous but shows a concentric lamination particularly towards the inner edge, it measures from 0·005 to 0·006 mm. in thickness.

At one point just opposite the centrosphere there is evidence of cellular structure.

The cytoplasm, fairly uniform in character, is separated from the inner wall of the Zona by what may be possibly a retraction cavity, some of the cytoplasm remaining adherent to the inner surface of the Zona.

The nucleus, of size approximately 0·03 × 0·022 mm., is fairly central in position, and has a faint and ill-defined nuclear membrane.

The arrangement of the chromatin is best realized by reference to the figure.

What appears to be the nucleolus breaking up is seen towards one end of the nucleus.

The nucleus is in part separated from the surrounding cytoplasm by a narrow cleft probably a retraction cavity though possibly it may be a space filled with fluid derived from the karyoplasm.

At one extremity of the nucleus lying within the cytoplasm *just outside* the *faint nuclear* membrane is a *small granule.*

Lying to one side of the nucleus and in contact with the nuclear membrane, which is here only faintly indicated, is a small sphere, 0·013 × 0·011 mm., consisting of a material so clear that it might be mistaken for a vacuole; it has, however, an obvious structure and contains near its poles two more darkly stained granules.

This object I take to be the Centrosphere, Attraction Sphere (Quain), Archoplasm Sphere (McMurrich), Centrosome (Robinson), Microcentrum (Heidenhain), Microsphere (Siedlecki), in the young oocyte sometimes called the Idiosome (corresponding to the attraction sphere of other cells). Van der Stricht identifies this with the Yolk nucleus or Body of Balbiani, as does Jenkinson[1], see also Wilson[2].

[1] *Vertebrate Embryology*, Oxford, 1913, p. 72.

[2] *The Cell in Development and Inheritance*, New York, 1900, p. 156.

Its contents are variously termed the Centroplasm or Archoplasm, whilst the granules are known as the Centrioles.

Other sections of this egg are available, but they exhibit nothing worthy of note. The appearance indicated in the figure, however, justifies us in assuming that the specimen represents the prophase condition in the Human Oocyte prior to the formation of the first polar body.

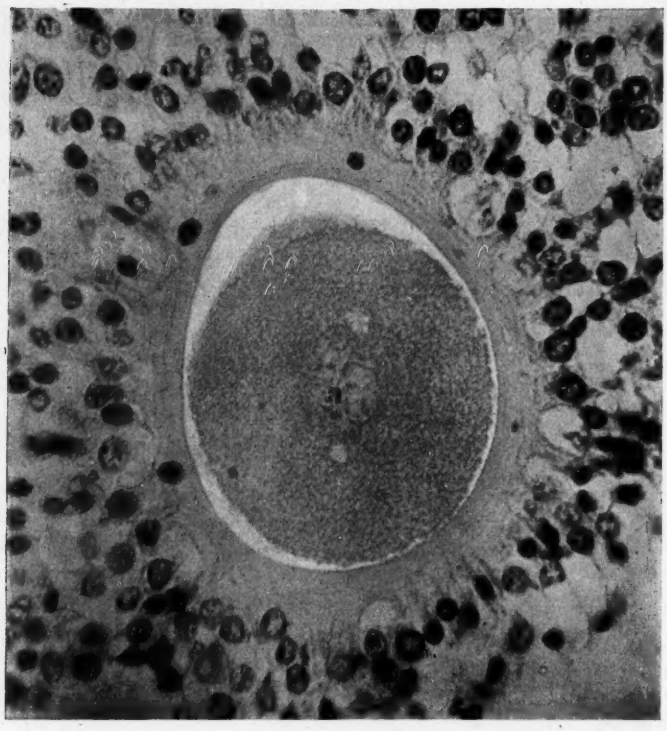

FIG. 2. Human ovum in discus proligerus in propnase of first division. × 600.

Fig. 2 shows an ovum in discus proligerus in Graafian follicle. Section 0·007 mm. thick. Stained with Ehrlich's acid haematoxylin and eosin.

Size including Zona 0·117 × 0·1 mm.; inside Zona 0·1 × 0·08 mm.

From a woman aged 22. Died of a femoral hernia. Same ovary as fig. 1.

The figure shows that the egg is not spherical.

The cells of the Corona radiata are here adherent to the outer side of the Zona pellucida by broader protoplasmic processes than in fig. 1, with arcaded spaces in between them, the summits of the arcades being directed to the Zona pellucida.

The Zona pellucida consists clearly of two layers, the combined thickness of which amounts to from 0·008 to 0·011 mm.

The three deeply stained bodies seen overlying the Zona pellucida are nuclei which have got floated over it in the process of mounting.

The inner zone is more homogeneous than the outer, it exhibits here and there evidence of a lamellar arrangement and at one or two points there seems to be distinct proof of the presence of cellular elements in its substance. At one pole it appears to be faintly striated radially.

This layer of the Zona pellucida I have reason to believe is the ovular layer.

The outer layer, continuous with the processes which pass to the cells of the Corona radiata is more open and fibrillar in structure. This I believe to be the ovarian layer of the Zona pellucida, the Zona thus being a compound structure made up of ovular and ovarian elements.

The cytoplasm, of granular appearance, is fairly uniform in density throughout. It is retracted from the inner surface of the Zona pellucida, the retraction cavity being slit-like for the most part, but increased in width towards one end, where it forms a considerable cavity, which is in part occupied by a faintly granular translucent material capping the substance of the cytoplasm at this end of the egg. This is possibly of the nature of a coagulum.

The nucleus measures roughly 0·02 × 0·017 mm. and occupies a position nearly central in the section of the cytoplasm. The nuclear membrane has disappeared, and the arrangement of the chromatin in scattered granules is best realised by reference to the figure. Some of these granules appear to fall in line parallel to the equator of the nucleus.

There is no evidence of a nucleolus, unless the presence of a larger chromatin granule denotes its presence.

The contents of the nucleus (karyoplasm) are everywhere confluent with the cytoplasm.

On either side of, and near, the nucleus are two small clear spots, each containing a highly refractive granule. In the specimen, these lie in line with the greatest diameter of the egg, but it is difficult to determine whether this corresponds with the true polar axis of the oocyte, since the example is taken from a specimen in which the serial sections are not complete.

These bodies, I take it, represent the divided centrosphere shown in fig. 1, each half containing its accompanying centriole. The divided centrosphere has now shifted its position so that its two halves come to lie on either side of the nucleus.

Other cytoplasmic inclusions. With the exception of a deeply stained granule lying some little distance to one side of the nucleus there is no apparent feature in the cytoplasm which calls for comment. I must leave it to those better versed in cytology to determine what the nature of this particle may be.

From the evidence before us we may, I think, assume that fig. 2 represents

a further stage in the prophase condition of the formation of the first polar body exhibited in fig. 1, the centrosphere there displayed having now divided into the two clear spheres each with a centriole and placed so as to lie on opposite sides of the nucleus, which now devoid of its membrane is approaching the stage when it divides.

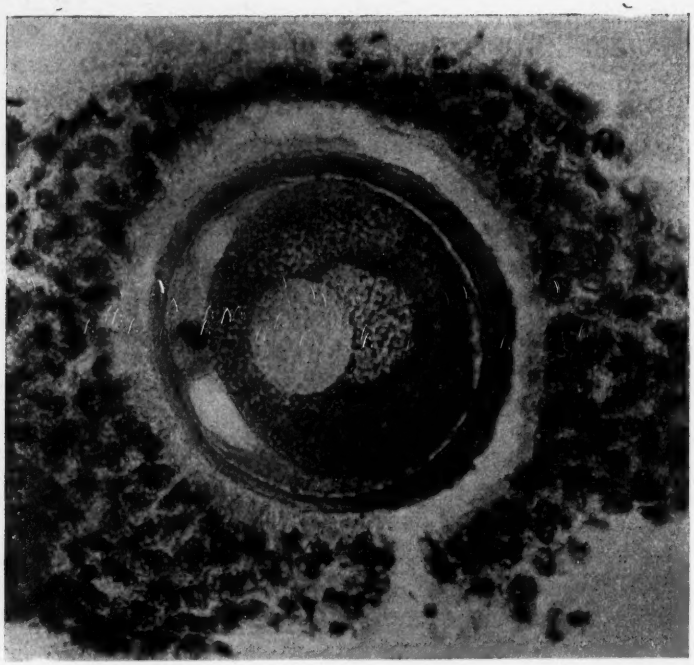

FIG. 3. Human ovum in discus proligerus in anaphase of first division and commencement of metaphase of second division. ×600.

Ovum in discus proligerus in Graafian follicle.

Thickness of section 0·01 mm., stained with Weigert's Iron Hæmatoxylin and Van Giesen.

Size including Zona 0·097 ×0·088 mm.; inside Zona 0·083 ×0·08 mm.

From a woman whose ovary was forwarded without any history, in the same case a morula and an ovarian blastula were found; these will be described in a subsequent paper. In this case the Fallopian tubes were much twisted and bound down by adhesions—presumably impervious to the descent of an ovum though apparently permitting the passage of spermatozoa.

The section here displays a more spherical appearance.

The cells of the Corona radiata are neither so discrete nor so clearly seen as in the previous figures (1 and 2). They are separated from the outer surface of the Zona pellucida by a zone about 0·001 mm. in width, which exhibits

but faint indications of structure, the fibrillar arcades being conspicuous by their absence and the tissue intervening, between the outer surface of the Zona pellucida and the innermost row of the cells of the Corona radiata on one side of the egg, appears but faintly striated and granular, whereas on the opposite side of the ovum the interval appears clearer as if occupied with fluid—further, there is a breach in the continuity of the girdle of surrounding coronal cells, as if by the penetration of the liquor folliculi, a stage, possibly, in the liberation of the oocyte from the cells of the discus proligerus immediately around it. It may reasonably be assumed that the arcading of the tissue connecting the cells of the Corona radiata with the Zona pellucida exhibited in the previous figures is part of the same process, brought about by the permeation of fluid (liquor folliculi?) in between.

The Zona pellucida on the two sides of the egg exhibits a marked difference in section, varying from 0·007 mm. on one side to 0·003 mm. on the opposite side of the ovum, a difference due no doubt to the obliquity of the section.

The innermost, more homogeneous and ovular (?) layer of the Zona pellucida alone remains, the external fibrillar or ovarian layer having now all but disappeared on one side, whereas on the other side it is reduced to a faint reticulum. The Zona pellucida left exhibits traces of concentric lamination with a suggestion at one point of cellular structure. In this specimen I can see no evidence of radial striation.

Within the Zona the cytoplasm has shrunk excentrically from the inner wall of the Zona pellucida, leaving on one hemisphere a considerable interval between the two, whereas on the opposite side it forms a linear cleft. This space is occupied by a fine clear granular material (coagulum?) exhibiting three large vacuoles. In the substance of this material at the point where the cavity is widest is a collection of chromatin grains arranged in nuclear form and associated on one side with a small sphere of granular matter, undoubtedly both combined being the first (?) polar body.

If this be so, and there can be little doubt of it, then the question arises whether this perivitelline space is an artefact or is a normal condition during life, in which a fluid liberated from the cytoplasm fills the space. If this be so, then the polar body, as seen in the section, will lie free in this fluid, and as it is presumably of greater weight than the liquid by which it is surrounded, this offers an explanation of how it sinks to one or other pole of the egg. As to which, there is some difference of opinion, for whilst most observers assign to it a position near the animal pole, Van der Stricht (see Quain[1], p. 11) on the other hand states that in the bat the polar bodies occupy a position which afterwards becomes the vegetative pole. If, as we are led to believe, the position of the vegetative pole is determined by the greater weight of the deutoplasm rotating the egg in that direction, then, if the explanation of the position of the polar bodies now offered be accepted, we have to some extent a confirmation of Van der Stricht's views, for the rotation of the egg and the

[1] Quain's *Anatomy*, vol. I. "Embryology," T. H. Bryce, London.

position of the polar bodies may both result from the same cause, viz. the action of gravity. There seems no evidence to show that the polar body always remains in the position in which it is extruded from the cytoplasm, and there is ground for supposing that the extrusion in an egg which is not truly spherical may take place at some considerable distance from the polar axis, the subsequent disposal of the polar body towards one or other pole of this axis being possibly determined in the manner suggested.

In this specimen the cytoplasm exhibits remarkable characters. We may assume that the appearance presented corresponds to the period immediately after the expulsion of the first (?) polar body, and that the contents of the oocyte display the phenomena associated with the anaphase condition of the first division and the commencement of the metaphase condition of the second division.

Three spheres are seen (the section was 0·01 mm. thick), lying, as may be seen from the overlap of their outlines, one in front of the other.

The anterior one, if such a term may be used in this connexion, is a relatively large vesicle (0·03 × 0·026 mm.) containing a clear faintly granular material, the only appearance of definite structure being two faint thread-like filaments of granular appearance lying close to and parallel with each other. The circumference of the vesicle is clearly defined from the surrounding cytoplasm. Behind this, and in part overlapped by it, is another spherical mass of approximately the same size. It consists of a mass of granular matter of darker tint than that contained in the vesicle just described, yet lighter than that of the surrounding cytoplasm. Scattered throughout its substance are numerous chromatin granules, not, however, so far as one can see, exhibiting any definite arrangement.

If this be the nuclear material of the daughter cell or Oocyte II, and there is every reason to believe it is, then it appears at this stage to be absolutely larger than the nuclei seen in figs. 1 and 2. The circumference of the nucleus, though clearly defined from the surrounding cytoplasm, exhibits no evidence of a nuclear membrane.

To the further side of the nuclear sphere, and in part covered by it, is a third spherical body of approximately half the size. The difference in size is misleading, for here it is cut unequally, as may be seen on examining fig. 4, which is the next section in series with it. In the present section this vesicle is only faintly differentiated from the surrounding cytoplasm, and little if any details of structure are observable.

There can be little doubt but that the structures here described are the nuclear material of the daughter cell in the middle with the two centrospheres on either side of it, though, as will have been gathered from the description given, these latter bodies exhibit no evidence of the fibrillation which one would expect to see at this stage; that, however, may be a very transient feature and one which does not militate against this assumption. The fact that the first (?) polar body is seen immediately outside these active changes

within the cytoplasm and nucleus, justifies us in thinking that the specimen has been sectioned immediately after the extrusion of the first polar body, and prior to the formation of the second polar body, the nuclear mass not having meanwhile undergone the changes associated with the resting condition which will succeed the extrusion of the second polar body.

Unfortunately the serial sections of this specimen are incomplete, so that it is well nigh impossible to form any opinion as to the position or direction of the plane of section, consequently it is difficult to determine whether the section passes through the ovum close to the equator or nearer one or other pole. For this reason the amount of the cytoplasm displayed in the section may consist of but a proportion of that contained in the widest diameter of the cell.

As displayed in the figure it will be seen that the cytoplasm on the two sides of the egg, at right angles to the position of the extruded polar body, differs in character and appearance, this may be due possibly to the unequal thickness of the section. On one side it appears darker, the granules appear more deeply stained, particularly along the circumference of the nuclear mass, whereas on the other side, the cytoplasm is less dense, though still darker than the substance of the nuclear mass, and exhibits a cloudy appearance.

In the substance of the cytoplasm between the smaller centrosphere and the periphery of the cytoplasm there is a small mass of more deeply stained substance at the other end of the axis of which the polar body forms one extremity.

As to whether this has any significance I must leave an open question.

Fig. 4, thickness of section 0·01 mm., stained with Weigert's Iron Hæmatoxylin and Van Giesen. This represents the appearance displayed by the contiguous section to fig. 3; it calls for less detailed description since it represents many of the same details of structure already referred to in fig. 3.

The essential points of difference are: *first*, that the section has passed above or below the position of the polar body, thus giving us a clue to its size. As the sections are 0·01 mm. thick it follows that the largest diameter of the polar body cannot exceed that measure; *second*, the material (coagulum?) filling the space between the cytoplasm and the Zona pellucida is uniform in structure, and the large vacuoles have disappeared; *third*, the size of the three spherical vesicles within the cytoplasm is more nearly equal, suggesting that they have been cut in the axis of the amphiaster. Associated with each lateral sphere, which, as we have already noted, is to be regarded as a centrosphere, may be seen a darkly stained granule, occupying a position, if not quite in the centre, at least near it.

These centrospheres are not so precisely defined from the surrounding cytoplasm as in fig. 3, nor are their contents so clear; but these are appearances which may be due to the density of the staining, or to the slight variation in the thickness of the sections.

The nuclear material of the daughter cell, which lies intermediate in posi-

tion between the two centrospheres, exhibits a granular appearance due to the presence of chromatin grains, some of which are arranged in thread-like fashion.

At one point in this mass there is however a definite clearly defined shield-shaped body, containing some highly refractive material, in the substance of which are a few more deeply stained granules. What the significance of this structure is I am not in a position to suggest.

The cytoplasm around the centrospheres and nuclear mass appears darker

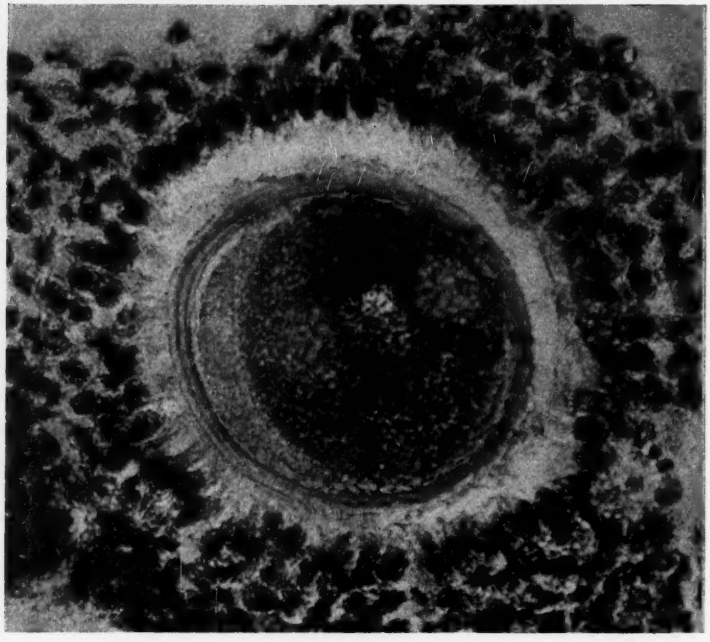

FIG. 4. Human ovum in discus proligerus in anaphase of first division and commencement of metaphase of second division. ×600.

on one side than the other, the darkest part lying in immediate relation to the nuclear mass on that side where the clear body within the nuclear substance is situated. On the opposite side of the nuclear mass there is a fairly large deeply stained granule. Around the centrospheres the cytoplasm appears more deeply stained, thus helping to define clearly the circumference of the spheres.

In the lighter hemisphere of the cytoplasm, three or four more distinctly stained granules may be seen towards the circumference of the cytoplasm.

The appearance of this section confirms in every respect the opinion set forth in respect of fig. 3, that the specimen represents the anaphase condition

of Oocyte II and the commencement of the metaphase condition and the formation of the second polar body.

Plate X provides a conspectus of a complete series of sections of an oocyte within the discus proligerus in a Graafian follicle from the ovary of a woman, aged 38, who died of heart failure, one day after admission to hospital.

There are 15 sections, each of 0·007 mm. thick, stained with Kernschwarz. In these the egg or its covering appears in 13 sections, so that from this the "thickness" of the egg at right angles to the plane of section may be estimated at 0·091 mm. The greatest diameter of the egg is met with in sect. 8, where including the Zona pellucida it measures $0{\cdot}11 \times 0{\cdot}1$ mm. In this section the diameters taken from the inner surface of the Zona pellucida measure $0{\cdot}093 \times 0{\cdot}083$ mm.

The cells of the Corona radiata are separated from the outer surface of the Zona pellucida by a clear space averaging about 0·006 mm. in width. Stretching across this space, numerous groups of fine fibres, with clear intervals in between them, are seen connecting the bases of the inner row of cells of the Corona radiata with the external surface of the Zona pellucida. The intervals between the bundles of fibres are apparently caused by the permeation of fluid (liquor folliculi?), and as will be seen in Plate X, the cells of the discus proligerus are being so separated up by the infiltration of the liquor folliculi, that the Corona radiata, so-called, is reduced to but a single row of cells in many parts of the sections shewn.

The Zona pellucida, of an average thickness of about 0·008 mm., is seen to consist mainly of the inner or ovular layer, the superficial layer, that formed by the felting of the fibrils derived from the deep row of cells of the Corona radiata, and consequently ovarian in origin, is now much reduced in thickness, and is apparently undergoing disintegration owing to fluid infiltration throughout it.

The inner layer of the Zona pellucida does not now exhibit any evidence of concentric lamination, but, as seen in sections 7, 8, 9 and 10, shows marked indications of radial striation. The change in the appearance of the Zona pellucida is so marked in this specimen, as contrasted with the earlier figure, as to suggest that some change in its structure is now taking place. It is worthy of note that the innermost layer of it is more dense or deeply stained, and in sections 7, 8 and 9, exhibits a clearly defined double outline. This appears to be due to no optical effect, but seems to be clearly structural. If this be so, we have to consider whether this is to be regarded as a distinct egg envelope—a vitelline membrane.

There is much confusion regarding the description given of the envelopes surrounding the egg. Bryce in Quain[1] mentions only the Zona pellucida. Robinson[2] in his diagram of the ovum and its coverings on p. 13, there indicates the vitelline membrane, as distinct from the Oolemma or Zona pellucida,

[1] Quain, 1908, vol. I. "Embryology."
[2] Cunningham, *Textbook of Anatomy*, 1913.

but he makes no mention of a vitelline membrane in the text, and consequently we are at a loss to know exactly what his attitude is regarding this layer. McMurrich[1] makes no mention of any layer other than the Zona pellucida, whilst Jenkinson[2] (p. 45) speaks of the ovum of vertebrates as "always immediately surrounded by a vitelline membrane, frequently termed a Zona pellucida," thereby implying that the two membranes are one and the same thing. Wilson[3] evidently regards the vitelline membrane as the equivalent of the Zona pellucida, whilst Paterson[4] defines the vitelline membrane as

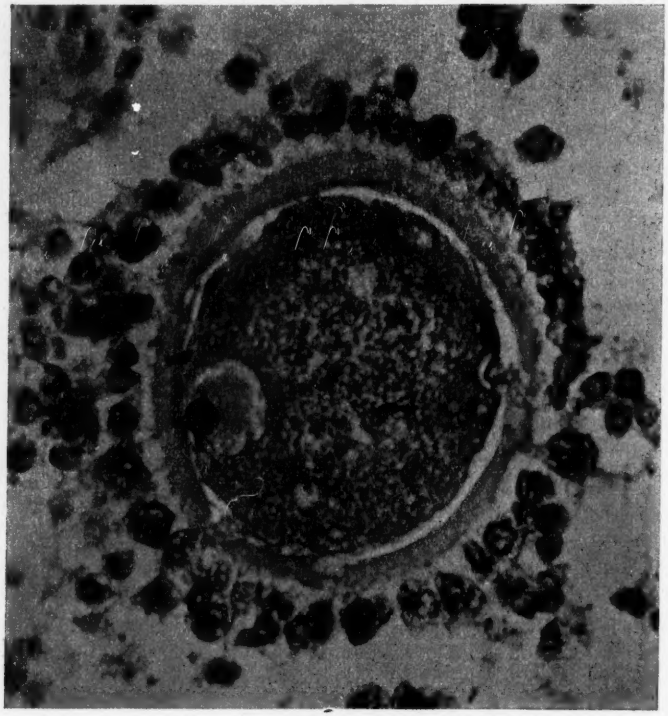

FIG. 5. Human ovum in discus proligerus exhibiting process of extrusion of the second polar body. ×600.

the proper cell wall of the ovum—"It is a clear, structureless membrane enveloping the protoplasm of the ovum, underneath the Zona pellucida."

The appearance here represented would seem to confirm the separate identity of these coverings of the egg. As we see it in this series of sections,

[1] *The Development of the Human Body*, 5th Edition, Philadelphia.
[2] *Vertebrate Embryology*, Oxford, 1913.
[3] *The Cell in Development and Inheritance*, New York, 1900.
[4] *Manual of Embryology.*

in some positions the vitelline membrane, if we reserve that name for the innermost covering of the egg as distinct from the Zona pellucida, is revealed by a double outline. In some sections its independent nature is clearly shown by its being stripped off from the inner surface of the Zona, whilst in places there seems evidence of cellular structure associated with it. It is from the inner surface of this layer that the cytoplasm retracts, forming, as we have suggested, a space occupied by fluid, and leaving on the inner surface of this membrane some small fragments of cytoplasm. This perivitelline space is of varying width, in places quite clear as if it had contained a fluid, and occupied here and there by what appear as extrusions from the cytoplasm. These points will of course be better seen in figs. 5, 6 and 7, where the structures are exhibited on a scale of magnification of 600 diameters.

The most remarkable feature exhibited within the body of the ovum is the excentric position of the nucleus or nuclear mass, as seen in section 8, of which a separate figure (fig. 5) is given.

In fig. 5, thickness of section 0·007 mm., stained with Kernschwarz, the nuclear mass abuts against the inner surface of the Zona pellucida, the vitelline membrane, if this be regarded as a separate structure, alone intervening. In this section the nucleus appears as if possessed of a distinct membrane, but this appearance is most probably an optical effect due to the difference in the refractive index of the material lying within the nucleus (the karyoplasm) and the cytoplasm. The karyoplasm, which is paler and less granular than the surrounding cytoplasm, is retracted, leaving a narrow space around it, this may be an artefact (the specimen was hardened in formol) or it may contain what has been described as the karyo-lymph or nuclear juice. Within the nuclear vesicle is a deeply stained granule measuring about 0·008 mm. in diameter, this exhibits a definite structure, having within it a paler sphere, to the side of which nearest the Zona pellucida is a more highly refractive granule. The whole nuclear vesicle measures 0·024 × 0·020 mm. The cytoplasm of the egg exhibits a remarkable appearance. Around its periphery it appears darker and more compact. Centrally, however, it becomes looser in texture, and the mitochrondrial grains stain deeper and stand out more clearly. Near its centre is a spherical granule possibly the centriole, and what seems like vacuoles occur within the substance of this less compact cytoplasm. The significance of this arrangement will be better understood, if now we examine the sections before and after this example.

Fig. 6 is a photomicrograph of section 7, of a thickness of 0·007 mm., stained with Kernschwarz. The central cytoplasm here exhibits a radial arrangement of its constituent elements which appear to converge towards the nuclear mass or vesicle, this appearance is emphasised by the disposition of the granules in filamentous threads, the extremities of these threads often seem to end peripherally in one or more deeply stained grains, frequently surrounded by a vacuole-like space, or clear interval, as if they were centres of some fluid secretion.

In this figure, these collections of clearer material are also seen to invade the more compact peripheral cytoplasm. As already stated, the filamentous granules converge towards the nuclear mass, in approaching which they form a denser or more compact zone in contact with the nuclear vesicle.

The nuclear mass consists of a paler, less granular material than the cytoplasm, within it are two deeply stained granules, whilst a third, of nearly similar size, lies on the circumference of the nuclear mass where it blends with the cytoplasm. There is no surrounding membrane, but the nuclear

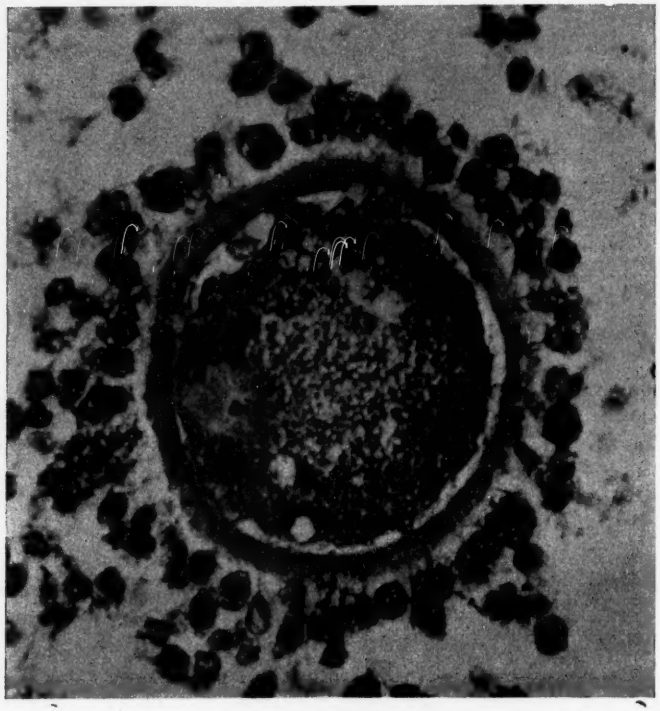

FIG. 6. Human ovum in discus proligerus exhibiting appearances associated with the extrusion of the second polar body. ×600.

material is pretty clearly defined from the surrounding cytoplasm. As seen in the figure the nuclear mass is placed on one side close to the inner surface of the Zona pellucida in contact with what I take to be the vitelline membrane; the surface of the nuclear material, so placed, appears clearly limited by a thin interrupted dark line.

There are one or two other details associated with the cytoplasm which may be noted. The circumference of the cytoplasm is here and there emphasised by what are evidently flattened layers of denser material which on

section show up as linear thickenings. That they are not optical in their origin is proved by their recurrence in the same situation in several sections. One of these is seen in fig. 6 a short distance above the nuclear mass. It recurs again in fig. 5 and again in fig. 7. A similar condensation of the cytoplasm on its periphery is similarly seen in these three sections on the side of the cytoplasm opposite the nuclear mass.

In fig. 6 there appear two rounded bodies lying in the perivitelline space,

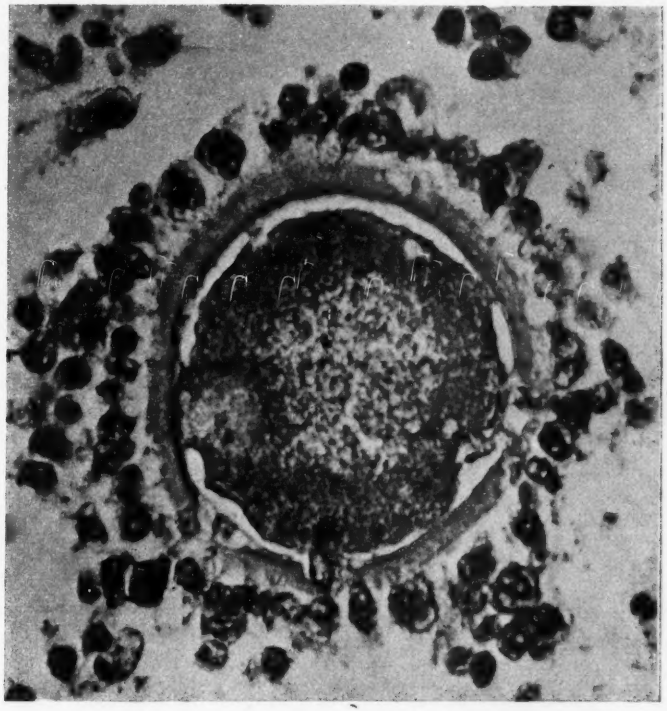

FIG. 7. Human ovum in discus proligerus showing the second polar body in process of extrusion. ×600.

one of which, the left, as is proved by an inspection of the section before fig. 6 (not here represented but seen in the plate showing the whole series) is evidently a part of the cytoplasm which has become separated off from the main mass. The other, the right, on localising it by the dial of the watch placed between 12 and 1, I am not so clear about. I am inclined to think that it is a cell of the Corona radiata which has got floated out of position in the mounting of the section.

Fig. 7 (thickness of section 0·007 mm., stained with Kernschwarz), is a

representation of the appearance of the section following fig. 5. I have placed them in this order for the sake of clearness and convenience of description. Here, the nuclear mass is seen in part pushing its way into the perivitelline space, it presents the same pale granular appearance already described, and contains in its substance two darkly stained granules, the one larger and more compact than the other. The part of the nuclear mass which is being forced beyond the periphery of the cytoplasm is clearer and paler in character, and exhibits distinct evidence of structure, there being a number of faint granules surrounded by clear spaces. Just as it passes the line of what we may regard as the circumference of the cytoplasm, this clearer mass is constricted so that the part of it pushed against the egg envelope is dumb-bell shaped in appearance, the remainder of this material, of somewhat spherical form, is bedded in the substance of the nuclear mass. The extruded part is accompanied by a small amount of cytoplasm. There can be little doubt that the appearance here observed corresponds to a stage in the extrusion of the second polar body. I say this with some confidence, for, as I shall presently show, there is evidence of the existence of the first polar body undergoing a state of division in this same oocyte.

The cytoplasm, as in the other figures, shows evidence of the same activity in the arrangement of its substance centrally, though here the radial arrangement is not so distinct, probably owing to the fact that it is cut tangentially, there does, however, appear to be some evidence that the darker granules are arranged in spherical form. About the position of 1 on the watch dial there is, near the periphery of the cytoplasm, a vacuole with a fairly large, deeply stained granule within it. The same vacuole is seen in the preceding and succeeding section; whether this has any significance, I know not, I note its presence, for now-a-days so many cytoplasmic inclusions are described that possibly it is well that the presence of this particular structure should be recorded.

As will be seen, the Zona pellucida in this figure has apparently been slightly damaged in the sectionising, but this is not without its advantages, for in the position of 7–8 on the watch dial there seems distinct evidence that, though there is a breach in the continuity of the Zona pellucida, its innermost layer is stripped off undamaged, a circumstance which would seem to confirm the belief in a vitelline membrane as distinct from the Zona pellucida.

From the description given—the figures must speak for themselves—there can be little doubt but that the appearances displayed correspond to the metaphase condition in the second division of the oocyte, and the phenomena associated with the extrusion of the second polar body.

The central mass within the cytoplasm corresponds to the mother centrosphere and spindle, the clearer material with its accompanying small amount of cytoplasm forced outwards against the egg envelopes is the daughter centrosphere, whilst, in between, we have the nuclear mass in process of undergoing division, though it must be confessed that the arrangement

displayed by the chromatin gives little clue to any definite arrangement of the chromosomes.

I have not hesitated to assume that the conditions here described are the changes associated with the extrusion of the second polar body, for, if now we turn to look at the plate of the entire series of sections we will there be able to note the presence in sections 3 and 4 of certain structures which we have every confidence in believing is the first polar body undergoing division.

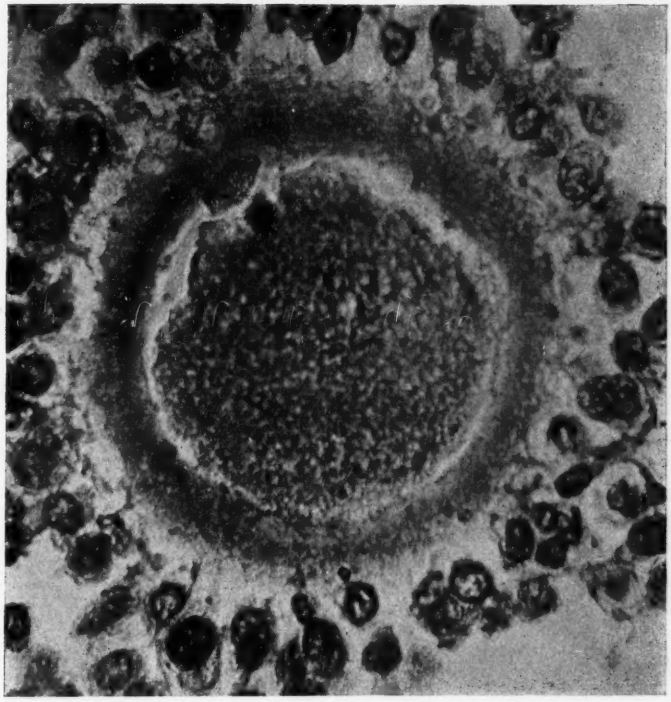

FIG. 8. Human ovum in discus proligerus, shows first polar body undergoing division in the ovum in which the second polar body is in process of being extruded. ×900.

In order to render this clearer I have introduced figs. 8 and 9 showing the details under a higher power of magnification. Before describing these, however, let me call attention to a point of some importance. Be it noted that the point of extrusion of the second polar body does not correspond to the position occupied by the first polar body. If we assume that the first polar body is polar in position (be it animal or vegetative pole) then the point of extrusion of the second polar body corresponds fairly closely to the equator of the egg, which fact helps to confirm the belief that the polar bodies,

once extruded, sink, by their own weight, in the perivitelline fluid to occupy the most dependent position within the egg envelope.

In fig. 8, which is a photomicrograph of section 4 of the entire series, 0·007 mm. thick, stained with Kernschwarz, magnified 900 diameters, there will be seen lying in the perivitelline space, which is here cut very obliquely, since it lies close to one of the poles of the egg, two distinct bodies in the position of 11 on the watch dial. One of these, the more external, is oval in

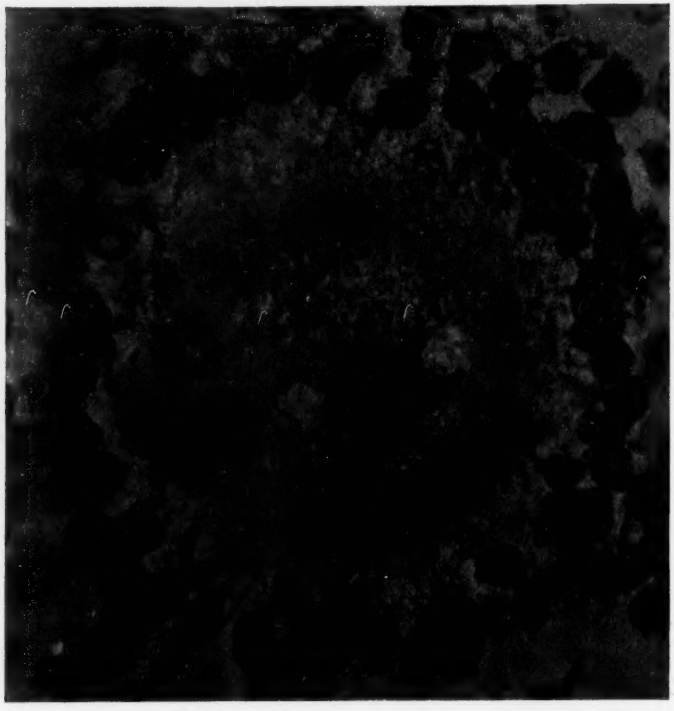

Fig. 9. Human ovum in discus proligerus showing first polar body undergoing division in the ovum in which the second polar body is in process of extrusion. × 900.

shape, rests on the egg envelope, and consists of a granular material containing fairly well marked deeper stained grains; at either extremity of the oval may be seen some of the chromatin aggregated together to form little spots of more compact granules. In this section, the oval body is separate and distinct from a darker mass lying between it and the cytoplasm, which in part overlaps it. This collection of deeply stained matter exhibits denser granules within it. If now we examine fig. 9, which is a photomicrograph of section 3 of the entire series, 0·007 mm. thick, stained with Kernschwarz, the section im-

mediately preceding that which is shown in fig. 8, we will see, in exact correspondence with the structures previously described in fig. 8, two deeply stained bodies containing chromatin granules arranged in such a way as to suggest that these are chromosomes; further the two bodies so described are seen to be connected by a bridge, which indicates their incomplete separation at this point. If these facts are admitted, and no other explanation seems possible, then I hold we have clear evidence that the structure we are dealing with is the first polar body undergoing division, coincident with the extrusion of the second polar body.

If this be so, we have in the series of sections of this oocyte a complete demonstration of the stages effected in the egg at the time of the extrusion of the second polar body. Further we have clear proof that in this oocyte, at least, the maturation stage associated with the discharge of the first and second polar bodies is completed within the ovary whilst the egg still lies within the discus proligerus of the Graafian follicle.

In Plate XI is reproduced the complete series of 16 sections (0·008 mm. thick, stained with Ehrlich's acid haematoxylin and eosin) of an oocyte within the discus proligerus, inside a Graafian follicle, obtained from the ovary of a woman aged 38, who died of heart failure twenty-four hours after admission to hospital. It was from the same subject that the examples already described under Plate X were obtained.

What strikes one at first is the size and shape of the egg.

The largest diameters are displayed in section 9 of the series, and are estimated as 0·113 × 0·1 mm. The corresponding diameters measured inside the Zona pellucida are as follows: 0·1 × 0·084 mm.

The egg and its envelopes run through 14 out of the 16 sections figured. As each section was 0·008 mm. thick, the total "thickness" of the egg sectionised amounts to 0·112 mm., so that the oocyte has evidently been cut transverse to its long axis, the two extremities of the egg as seen in the serial sections will correspond therefore to the poles, if these are determined by its longest diameter, a point of some importance in regard to the disposition of the polar bodies, and one concerning which Jenkinson[1] makes the definite statement that "In cases where the egg is ovoid or ellipsoid (Myxinoids, Amia) the egg axis is the major axis."

The diameters given for this oocyte, which is in a very perfect state of preservation, preclude the possibility of it being described as spherical. A matter worth drawing attention to is that this oocyte exceeds by an appreciable amount the diameters given for those already described.

The cells of the discus proligerus or cumulus, which immediately surrounds the egg to form the Corona radiata, are closely packed, only at one point is there a breach in their continuity shown in sections 6, 7, 8 and 9. Here the liquor folliculi, shown in the photomicrographs as a pale granular-looking coagulum, is free to enter, and has evidently bathed the external

[1] *Vertebrate Embryology*, Oxford, 1913, p. 40.

surface of the Zona pellucida, though as yet in this specimen it does not appear to have extended much by infiltration between the outer surface of the Zona pellucida and the deeper row of cells of the Corona radiata. In consequence, the fibrillar substance, cementing the innermost cells of the Corona radiata to the outer surface of the Zona pellucida, and forming by its "felting" the outer or ovarian layer of that membrane, is more compact, and not so broken up by fluid infiltration as that described in the previous examples.

The Zona pellucida, of an average thickness of from 0·006 to 0·008 mm. is very well seen in many of the sections, particularly in Nos. 7 and 8, where its separation into an inner and an outer layer is very clearly seen, the outer being obviously of a different character from the inner and being formed by the felting of the basal fibres of the innermost cells of the Corona radiata and therefore ovarian in derivation, whilst the inner layer, clearer and more homogeneous, and derived, as I have reason to believe from a study of the growth period of the oogonium, from the ovum itself (I hope to publish this series of observations later), is limited internally by a well defined line, which on careful examination is seen to be double. This, I take it, is confirmatory of the view that internal to the Zona pellucida, and in contact with it, there is another egg membrane, the true vitelline membrane of which I have already spoken. The ovular or inner layer of the Zona pellucida proper exhibits appearances here and there which suggest concentric lamination; in other situations, in some of the sections, there is an appearance of radial striation, but I have not been able to observe any of the fibrillae derived from the inner cells of the Corona radiata traversing the substance of the Zona pellucida. In one or two instances, notably in section 7, there are evidences of cellular formation or cell inclusions within the substance of the inner or ovular layer of the Zona pellucida.

As has been already suggested, there appears to be evidence of a layer within the Zona and adherent to it, which is possibly a true vitelline membrane, but in these sections it must be admitted that the evidence is not very convincing, for it is extremely difficult to make out whether the appearance is due to an optical effect or no.

The cytoplasm in all the sections exhibits an evenly granular appearance, increasing in density in the centre and around the nucleus. This central darker mass is separated, here and there, from the surrounding lighter cytoplasm by a more open grain in the granular material, amounting in places to definite irregular clefts, whether this appearance is due to the influence of the hardening agent (formol) or is a natural condition induced by excess of fluid is a moot point.

In most of the sections the cytoplasm appears to fill completely the egg envelope, but if the middle sections of the series, viz. those near the equator of the egg, be carefully examined there is definite evidence of a narrow interspace between what Waldeyer has called the oöplasm cortex, i.e. a narrow

zone of finely granular material surrounding the cytoplasm, and the inner side of the egg envelope. This space, the perivitelline space, for such it would appear to be, is probably filled with a fluid extrusion from the cytoplasm, for in it appear two or three bodies which will now be described.

In sections 13 and 14 of the series, close to the pole at that end of the egg, are seen to be certain conspicuous features. In section 14, here shown in fig. 10, there are two distinct nuclear granules surrounded by an irregular

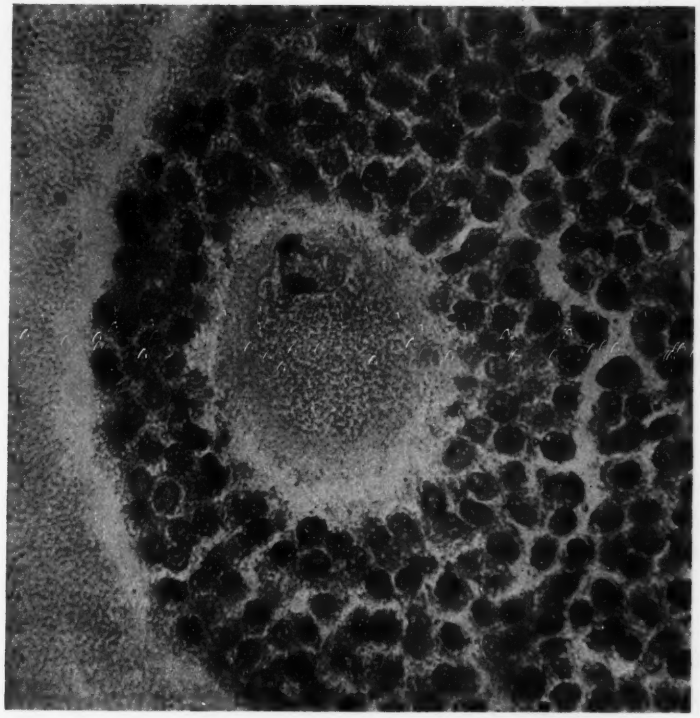

FIG. 10. Section of a mature human ovum in the discus proligerus showing near one of its poles the now divided first polar body. ×600.

mass of slightly darker material than the adjacent cytoplasm. This substance is also faintly indicated in the previous section (not here figured).

From a careful study of this object I think there can be little doubt but that we have the first polar body in a divided condition. It will be noticed that so far as its site is concerned it is distinctly polar in position, that is to say it lies at one extremity of the greatest diameter of the egg.

Having thus accounted for the first polar body it remains to determine the existence of the second polar body. In doing this considerable difficulty was experienced, as there were sundry objects which might be taken for it,

but after careful examination I am inclined to believe that the structure exhibited in section 7 of the series, opposite 11 of the watch dial, is the object we are in search of—the second polar body (fig. 11). Here is seen a darkly stained granule of chromatin which on high magnification resolves itself into more or less distinct groups of chromatin particles apparently connected together, the whole being surrounded by an envelope of a substance identical with that of the adjacent cytoplasm. If this be the second polar body, it

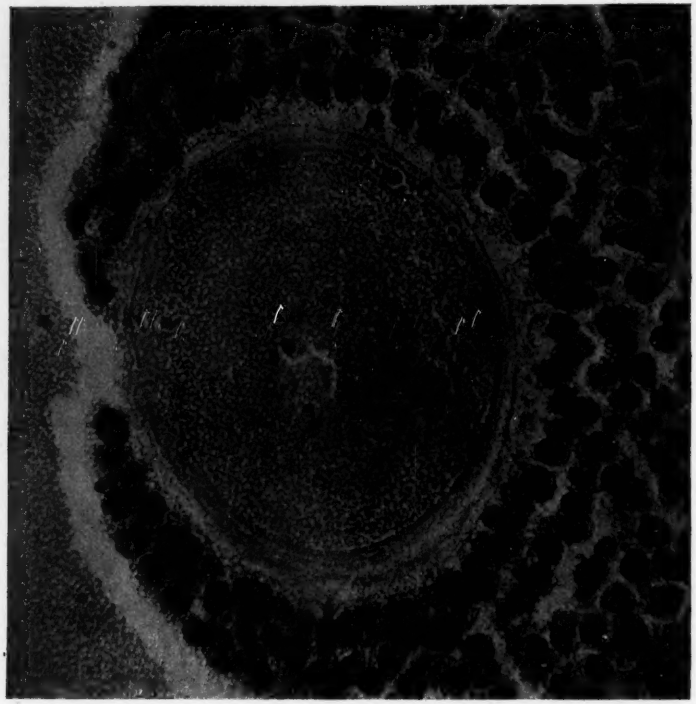

FIG. 11. Section of a mature human ovum in the discus proligerus showing in the direction of 11 of the watch dial the second polar body within the zona pellucida. ×600.

should be noticed that its position does not correspond to that of the first polar body. As to whether it may ultimately sink to the same position as that occupied by the first polar body is a matter of surmise, evidently, like that described in the last figure, it is extruded from the cytoplasm at a very different level from that now occupied by the first polar body.

All the other deeply stained bodies, which one might have associated with a polar body, have been eliminated, for the reason that they are evidently washed granules in the process of mounting. There still remains the fact, however, that, here and there, along the inner surface of the envelope covering

the left hemisphere of the egg, there are bulla-like extrusions from the substance of the cytoplasm, forcing their way into the Zona pellucida across the perivitelline space. The contents of these blister-like bodies seems less solid and granular than the material of the cytoplasm.

That this appearance is the result of a vital act is suggested by the evident approach of vacuoles towards the surface of the cytoplasm seen at 10 and 11 of the dial face in section 8, where one of them contains a deeply stained

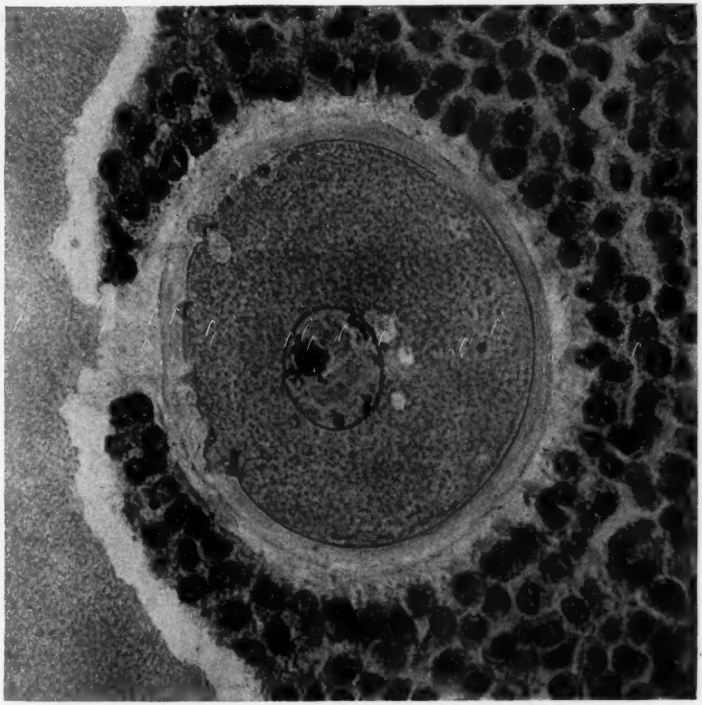

FIG. 12. Section through a mature human ovum in the discus proligerus: the polar bodies of this ovum have already been shown in Figs. 10 and 11. ×600.

granule. It would seem as if these vacuoles were on their way to reach the perivitelline space, there to discharge their contents.

The nucleus, 0·03 × 0·024 mm. in size, has returned to a nearly central position in the egg, it is surrounded by a faint and delicate membrane, somewhat unduly emphasised in the photograph shown in fig. 12.

These facts, taken in conjunction with the undoubted presence of the first polar body, afford convincing proof that the oocyte has passed to the resting stage of the mature egg, and that already the phenomena associated with the extrusion of the second polar body have been passed, since we are led to

believe, on the evidence of those familiar with the changes occurring in other mammalian ova, that there is *no resting stage* between the *first and second maturation* divisions, hence the necessity for a search for the second polar body. If the present assumption be true, all these facts seem to harmonise and amply justify us in establishing the identity of the second polar body already referred to. Herein we have therefore to deal with a mature oocyte provided with what is now the female pronucleus. The nucleus, so described, as it appears in the figure (fig. 12) has a deeply stained spherical nucleolus 0·007 mm. in diameter, lodging a more refractive granule within it. The nucleus contains, besides, in the finely granular karyoplasm a number (about 15 in this figure) of small chromatin granules mainly disposed around the nucleolus, and lying, too, along the inner side of the nuclear membrane.

The karyoplasm is traversed by irregular clefts, whether artefacts or vital features it is impossible to determine.

In the preceding and succeeding sections in which the nucleus is cut and appears, the nuclear membrane in the photographs is faint but distinctly traceable.

In the section just before fig. 12, the nucleolus is also represented by a thin slice, and scattered through the karyoplasm of the three sections are chromatin granules to the approximate total number of 45 to 50. Some of these appear to be isolated grains, some linked together in threads, and others arranged in groups.

Around the nucleus, externally, and lying either near, or in close contact with, its membrane, are sundry vacuole-like bodies. Three of these, of varying size, each with a faint granule in it, lie opposite to the upper right quadrant of the nucleus. Another, not so clear, lies in the direction of 5 of the dial face.

In section 9 of the Series Plate XI (shown in fig. 13) a larger vesicle, 0·012 × 0·008 mm. in size, lies in the direction of 3 of the watch dial, in contact with the nuclear membrane. Its contents are clearer than the surrounding cytoplasm, and more finely granular, possibly this may be the remains of a centrosphere.

What the significance of the other structures may be, I know not, but their constant recurrence in other ova which I have studied suggest that they are normal features associated in some way with the nutrition or activity of the egg.

There can be little doubt, I think, that the oocyte above described has reached its mature condition. All the facts seem to justify this assumption.

The presence of a divided first polar body, the withdrawal of the nucleus to a central position, the reappearance of the nuclear membrane and the nucleolus, the probable identity of the second polar body, and the disappearance of all activity on the part of the centrospheres, all point to the correctness of this conclusion. It may further be added that judging by the thinness of the overlying ovarian layer, this oocyte was found in a Graafian follicle at a stage which must have been close to the period of rupture.

Plate XII represents a complete series of 12 sections (0·008 mm. thick, stained with Weigert's Iron Hæmatoxylin and Van Giesen) of an oocyte in the discus proligerus, inside a Graafian follicle, from the ovary of a woman aged 38 who died of heart failure one day after admission to hospital. This is the same subject as that from which the specimen figured in Plate XI was obtained.

The largest diameters, 0·111 × 0·09 mm., are seen in section 5 of the series. Measured from within the inner surface of the Zona pellucida the corresponding diameters are 0·10 × 0·08 mm.

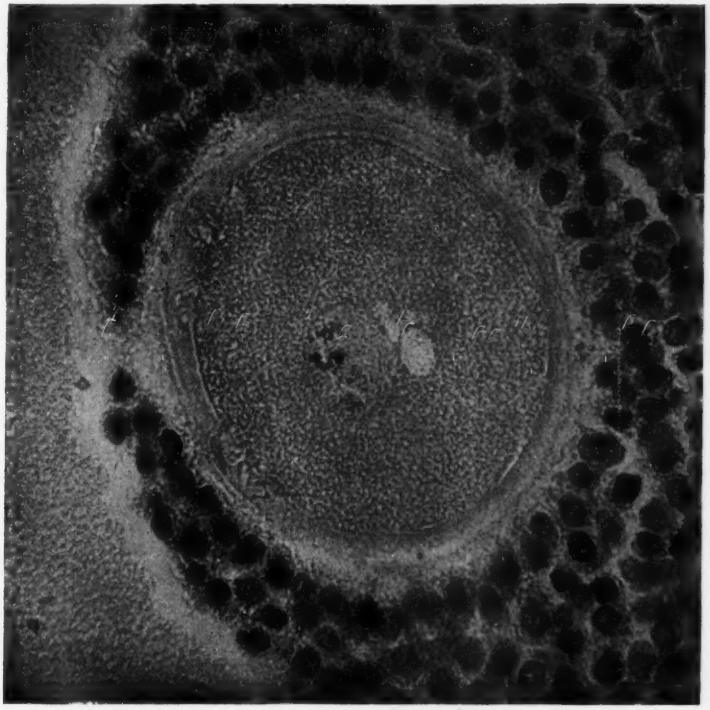

FIG. 13. Section through a mature human ovum in the discus proligerus, the vesicle to the right of the nucleus may possibly be the remains of a centrosphere. × 600.

The egg and its envelopes run through 10 of the 12 sections, and as each section was cut to a thickness of 0·008 mm., the total diameter of the egg as estimated by taking the total thickness of the 10 sections amounts to 0·080 mm., so that the inference is that the sections displayed in the plate have been cut in a plane parallel to the long axis of the egg.

In this instance, also, the egg, which is in a good state of preservation, can in no sense be described as typically spherical.

This specimen is much of a size with that described in connexion with Plate XI.

The cells of the Corona radiata towards the middle of the series are seen to consist of a single layer augmented here and there by cells forming a second row, but it is evident from an inspection of the figures that this combined layer is separated from the surrounding loosely arranged cells of the discus proligerus by intervals of varying width occupied doubtless by liquor folliculi. It is interesting to note that the coagulum formed by the liquor folliculi seen towards the edges of the lower sections is of an open fibrillar nature as contrasted with that seen in the last series of sections (Plate XI). The significance of this difference is difficult to determine, for both specimens were fixed with the same reagent (formol); presumably it is due to some change in the constitution of the fluid.

There are occasional breaches in the continuity of the inner row of coronal cells, so that ample channels are available for the free permeation of the fluid between the inner layer of cells of the Corona radiata and the outer surface of the Zona pellucida. In consequence we see that the fibrillar matter connecting the cells of the Corona radiata with the outer surface of the Zona pellucida is much broken up, the bundles of fibrils being separated by interspaces of varying width, thus providing free access for the liquor folliculi. In consequence only a feeble connexion is established between the Zona pellucida and the cells of the Corona radiata—so also the outermost layer of the Zona pellucida formed by the felting of the fibres derived from the coronal cells is considerably reduced in thickness.

The Zona pellucida, of an average thickness of from 0·004 to 0·005 mm. in the sections where it is cut transverse to its surface, is mainly composed of the inner homogeneous or ovular layer, the outer or ovarian layer as just described is relatively thin. The Zona pellucida has been variously described as a firm, tough, and elastic membrane. I confess that in my observations on the human ovum, limited it is true to hardened specimens alone, this account ill accords with what one sees, for the frequency with which various objects in contact with it indent its surface, rather belies this description; it would seem to me to be of a more plastic nature than is usually described. It may of course be that the erosions in its substance are caused by the vital activity of the material in contact with it. In the sections which are meridional there is evidence of a clearer layer in contact with the inner surface of the Zona pellucida as indicated by quite definite outlines and paler tint. This, if our surmise be correct, is the vitelline membrane proper, though in this specimen there is no indication of its independent nature by being separated or torn away from the Zona pellucida. In the sections close to the meridian the inner layer of the Zona pellucida occasionally presents faint indications of a concentric laminated arrangement, it is only in the region of the lower pole of sections 5 and 6 that a faint radial striation is reproduced in the photographs.

The cytoplasm is retracted from the vitelline membrane, to which some few particles of its substance still adhere, to form a perivitelline space, well seen in many of the sections.

In sections 4, 5 and 6, in the position of 1 of the watch dial a considerable mass of the cytoplasm, clearly fragmented, has been pulled away from the general substance of the cytoplasm as if here its attachment to the vitelline membrane had been more intimate, a circumstance which suggests that the cavity is due rather to an artefact than to a vital process. The reader may be

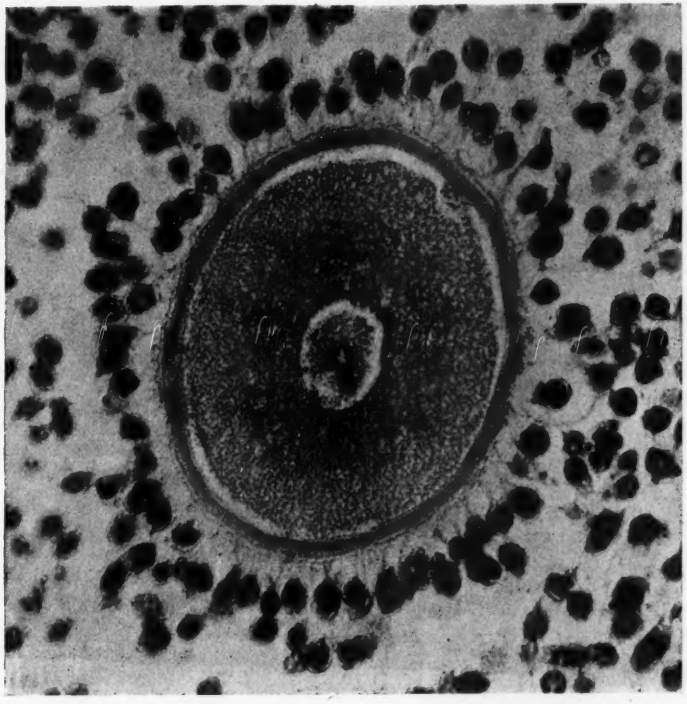

FIG. 14. Section through a mature human ovum in the discus proligerus. ×600.

reminded, however, that in previous examples (figs. 2, 3, 4) we have seen this space occupied by a coagulum, a condition which presupposes its existence during life.

The cytoplasm displays an evenly granular appearance, gradually increasing in density and tint towards the central area of the cell and around the nucleus. The darker zone, however, is not of uniform appearance, but has a mottled look due to the alternation of lighter and darker material. It is noticeable too that in sections 5 and 6 the darker material seems to radiate out into the peripheral cytoplasm by pointed strands. Here and there through-

out the cytoplasm in general may be seen a few more deeply stained granules. Towards the circumference in section 6 there is a suggestion of the granular material being arranged in radial threads.

The nucleus, 0·028 × 0·022 mm., best seen in section 5 (fig. 14), is there shown all but central in position. It by no means follows, however, that it is central in the egg, for whilst there are three sections antecedent to it, there are six sections following it. In section 5 it exhibits a distinct membrane, possibly emphasised in the process of reproduction by photomicrography,

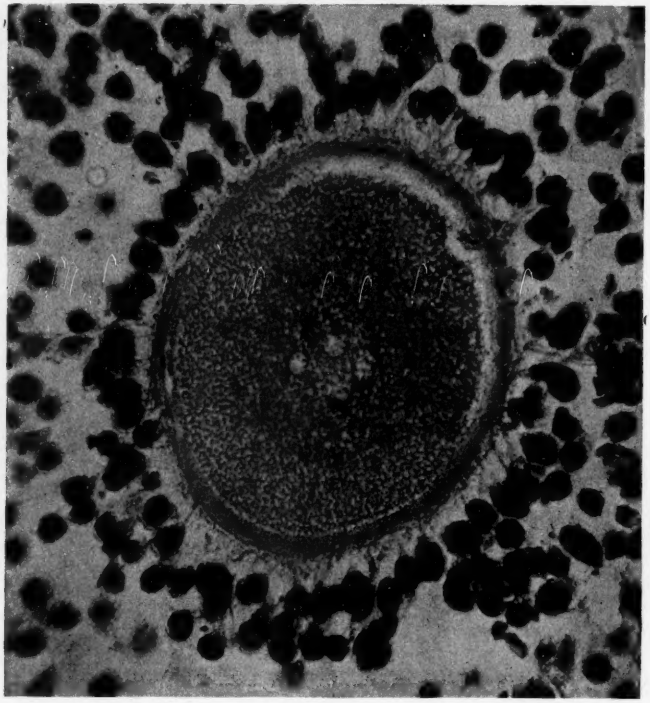

FIG. 15. Section through a mature human ovum in the discus proligerus showing vesicular appearance within the nucleus. × 600.

but undoubtedly revealed on microscopic examination as a distinct clearly defined covering. In the serial sections on either side of section 5 the nucleus is again cut, but there, in the photographs, there is but slight indication of a nuclear membrane. This does not necessarily imply that the membrane is not there, for experience has taught me that so delicate a structure is very difficult to define, particularly when it is cut obliquely. Careful examination, however, in both these sections reveals a faint indication of its presence.

Within its membrane, as shown in section 5 (fig. 14), the karyoplasm of

the nucleus has shrunk from its envelope, leaving a clear space presumably occupied by karyolymph. The mass of the contained karyoplasm is faintly granular and contains numerous chromatin granules, some single, some in pairs, and some arranged in filaments; whilst one mass, thicker and of elongated form, near the centre of the nucleus displayed in section 5 may be described as a chromosome. Whilst many of these chromatin particles appear in the substance of the karyoplasm, a number are shown closely applied to the inner surface of the nuclear membrane.

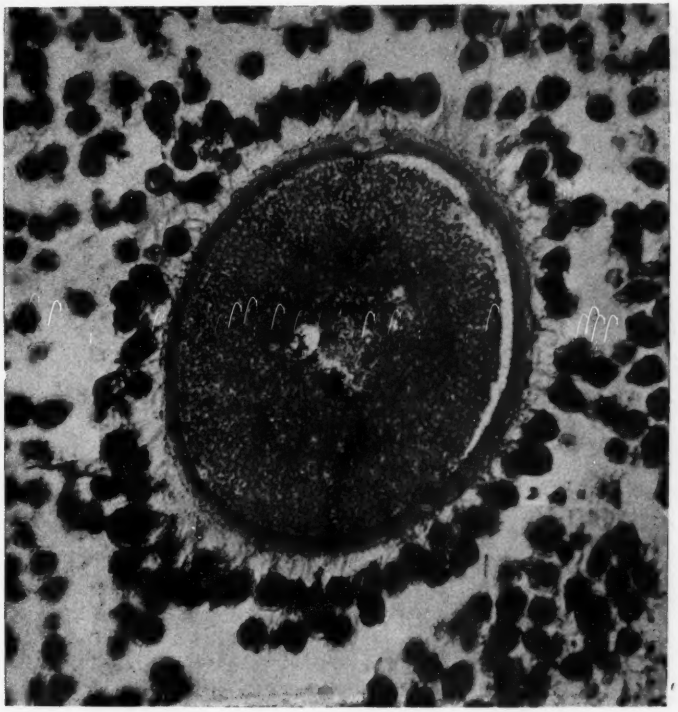

FIG. 16. Section through a mature human ovum in the discus proligerus. Note the occurrence of the clear vesicle containing darkly stained granules to the left of the nucleus. × 600.

In the three sections dividing the nucleus seven filamentous threads, seven paired granules, and ten isolated grains may be noted besides the chromosome referred to, and in addition a more or less compact mass of granules shown at the lower end of the nucleus in section 6.

In connexion with some of these granules there appear little vesicles which would seem to be filled with the products of their activity, of these three or four may be seen in section 4 and one in section 5 (section 4 is shown in fig. 15).

In section 6, reproduced in fig. 16, to all appearance outside the nucleus, but in contact with it, is a remarkably clear vesicle 0·01 × 0·006 mm., lying in the direction of 9 of the watch dial ; within it peripherally and also directed to 9 of the dial is a single chromatin granule, to the 5 dial side of which is a curved wreath of Λ-shaped chromatin particles. What this is is matter for speculation. It will be discussed later.

Near the nucleus in section 6, in the direction of 2 of the dial there is a group of small pale vesicles, three in number, embedded in the substance of

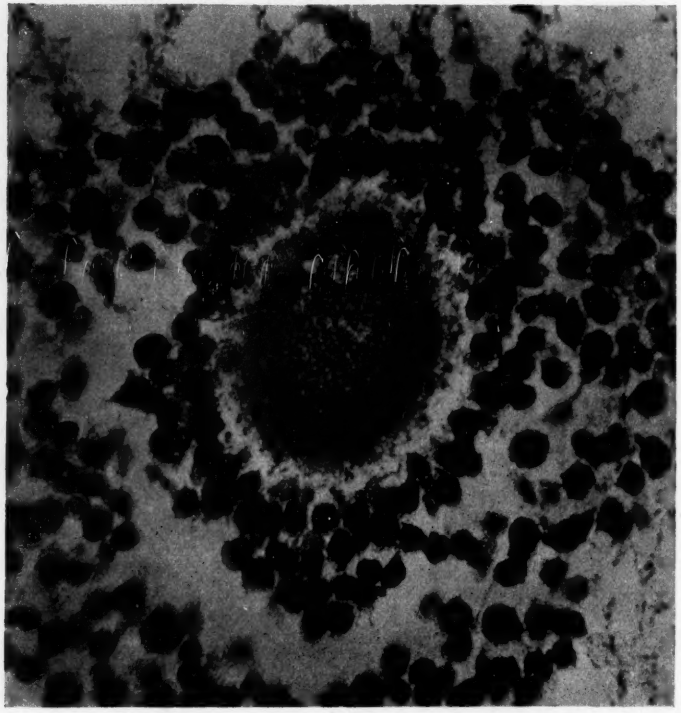

FIG. 17. Section through a mature human ovum, showing, in the direction of 12 of the watch dial, the first polar bodies. × 600.

the central cytoplasm; each exhibits an appearance of structure within, and each is fairly clearly defined from the surrounding structure.

The recurrence, at the pole of the egg (see section 10 of the series, reproduced in fig. 17), of a feature closely resembling that which in corresponding position in Plate XI we have identified as the first polar body, suggests a similar explanation of the appearance here seen. In the section lying between the cytoplasm and the egg envelope in the direction of 12 of the dial is an object composed of granular substance and more deeply stained material

evidently composed of chromatin particles. If now section 9 be examined in the corresponding position two (or it would almost appear three) fairly clearly defined oval-shaped bodies are seen. The appearance exhibited in these two sections, though not so definite and typical as those displayed in the figures already given (fig. 10), is yet sufficient to justify us in assuming that the appearance here described is none other than the first polar body in a divided condition. If this be not admitted we are forced, in face of the confirmatory evidence, to supply a better explanation of its presence, that I confess I cannot do, since it is obviously not due to any defect in the cutting or mounting, we are left with the alternative of accepting the only feasible explanation, viz. that it is the first polar body.

Accepting this as a fact, then we have to take in connexion with it the obvious detail that the nucleus is more or less central, that there is a nuclear membrane, and that the centrospheres have disappeared, in other words that the nucleus is now returning to the resting stage. If so, we are in duty bound to look for the second polar body. At first sight one was inclined to assume that the fragmented mass of cytoplasm already referred to in sections 4, 5 and 6, as occupying the perivitelline space was the body in question, but careful microscopic examination, emphasised by the microphotographs themselves, puts it beyond a doubt that this appearance is to be explained as an artefact. The other alternative presented is shown in section 8 (fig. 18), where apparently lying on the surface of the Zona pellucida there is a collection of granules in the direction of 8 of the watch dial. It must be remembered that here the egg envelope is being cut obliquely, so that the appearance of the object here represented as more or less embedded in the substance of the Zona pellucida is misleading. It rests rather on the inner sloping surface of the egg envelope, and lies appropriately in what is the perivitelline space, no longer visible owing to the oblique manner in which the structures are cut. Again, though not so typical as that previously described in fig. 11, it would appear, for lack of a better explanation, that the object referred to is none other than the second polar body. In point of structure it appears as four fairly large spherical granules, two darkly stained and two clearer, the latter lying between and partly overlapped by the former. The position occupied by this body is separated by one clear section 0·008 mm. thick from the plane of section of that containing the first polar body. Further, be it noticed, that it lies almost at the opposite side of the egg, occupying a position corresponding to 8 of the dial, whilst the first polar body lies in the direction of 12 of the dial. There is no evidence to show the point where the second polar body was extruded from the cytoplasm, it only appears, that at the present stage, its position does not coincide with that of the first polar body, as we have been led so frequently to believe.

If we accept the above description as satisfactory, in so far as it establishes the identity of the first and second polar bodies, then we have to explain the occurrence of the remarkable body seen to the 9 dial side of the nucleus in

section 6 (fig. 15) to which attention has been already directed (p. 52). The chromosome-like characters of the contained chromatin, and their arrangement in wreath-like fashion in the equatorial zone of the vesicle, appear to suggest that we are dealing with some nuclear structure in an active division phase, but what it may be, if this be granted, is a mystery, for there is evidence that it lies outside the membrane of the nucleus of the egg, and there is no appearance of any centrosphere activity around it. For the present I must leave it at that, frankly admitting that in the present

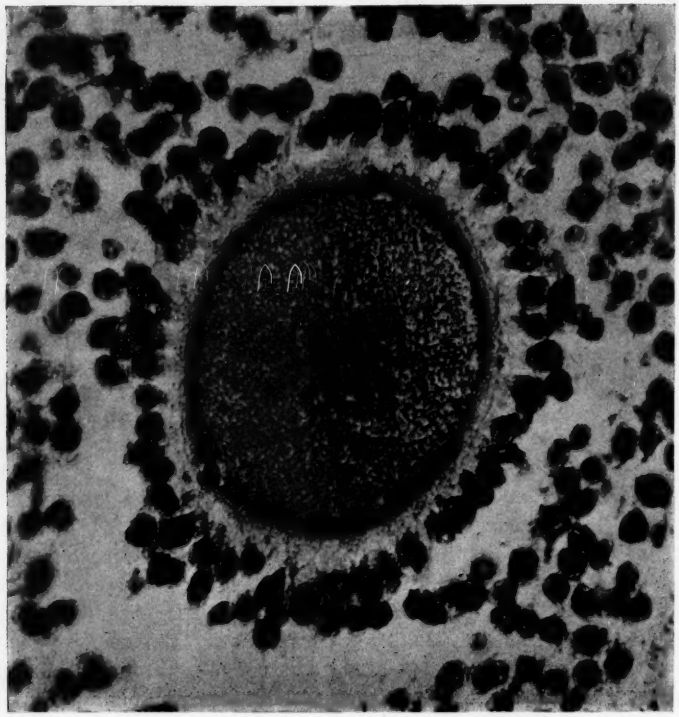

FIG. 18. Section through mature human ovum in the discus proligerus, showing in the direction of 8 of the dial, what is regarded as the second polar body. ×600.

state of my knowledge of the subject its presence is inexplicable. It may be a coincidence, but the fact is worth recording that in section 9 of series Plate XI, there is in the direction of 3 of the dial a vesicle of much the same size lying in contact with the nuclear membrane. In that case, however, there are no chromatin contents. Is it possible that these two structures are similar and represent a phase in the disappearance of a centrosphere?

From the facts observed, this oocyte, like the last one described, is most

probably in the mature condition. Its nucleus is now the female pronucleus, and since the identity of the first polar body has been fairly convincingly established we are justified in assuming that taking into account the more or less central position of the nucleus, and the fact that it has now resumed its nuclear membrane, the egg has passed beyond the phase in which the second polar body was extruded and is now in the resting condition of the mature oocyte. This is an additional reason for assuming that the object identified as the second polar body is in fact that structure.

On carefully tracing the Graafian follicle, in which the ovum was contained, its wall was found of a thinness which would suggest that its early rupture could not be long delayed.

RESUMÉ

Reviewing the facts and their interpretation as expressed in the previous pages, we may summarise the results as follows:

1. The human egg is not a sphere but an ovoid structure.

2. *Size of the Human Oocyte.* The diameters of the various examples described are here tabulated.

	Including Zona pellucida (mm.).
Oocyte Fig.1	0·1 ×0·09
Oocyte Fig. 2	0·117 × 0·1
Oocyte Fig. 3	0·097 × 0·88 thickness.
Oocyte Pl. I	0·111 × 0·1 ×0·091
Oocyte Pl. II	0·113 × 0·1 ×0·112
Oocyte Pl. III	0·111 × 0·09 × 0·08

The variation in size is very slight, and apparently there is no evidence to indicate that a change in size occurs during the maturation period. My measurements are considerably less than those usually quoted.

3. The character of the Zona pellucida appears to undergo a process of thinning, by the dissolution of its external ovarian layer, by means of which it is intimately connected with the inner cells of the Corona radiata. The reduction in the thickness of this layer is evidently effected by the permeation of the liquor folliculi through its substance, thereby leading to a separation of its elements into strands or small groups of fibrils which at the period of expulsion of the oocyte may be easily ruptured.

4. There seem grounds for believing that lining the inner surface of the Zona pellucida there is a structurally distinct layer, the vitelline membrane proper. The evidence in support of this view is that in a case (fig. 7) in which the Zona pellucida was torn across, this fine inner layer remained intact, further the occurrence of a faint double outline exhibiting a paler structure within seems to point to the independent nature of this membrane.

5. The Zona pellucida, whilst generally speaking homogeneous in character, yet exhibits in some instances a faint appearance of concentric lamination. From the observations on the specimens here recorded it would seem as if the radial striation only occurred in the later stages of the maturation of the

oocyte, but I hesitate, on such slender evidence, to lay stress on this. Within the substance of the zona there appears from time to time the suggestion of fine cellular elements. I have not yet been able to trace the fibrils from the cells of the Corona radiata through the substance of the Zona pellucida as some have described. The thickness of the Zona pellucida ranges from 0·003 to 0·011 mm., yielding as an average a little over 0·006 mm.

6. *The perivitelline space.* The existence of this space has been a matter of much controversy. The strongest evidence I can produce in its favour is the presence of a distinct coagulum within its cavity (see figs. 2, 3, 4, and pp. 177, 179, 181). Its greatest development appears to coincide with the extrusion of the polar bodies which eventually come to lie within it. After the expulsion of the polar bodies the cytoplasm appears to fill the egg envelope more completely.

7. In the cytoplasm the appearance of a single centrosphere has been recorded. This is again shown divided and placed on either side of the nucleus in fig. 2, the two parts resulting from this division are again represented in fig. 3 as well defined spherical masses. In a later stage the central part of the cytoplasm is evidently affected by the centrosphere (fig. 4). Later, after the extrusion of the second polar body, the centrosphere seems to be associated with the regrouping of the denser central cytoplasm. Finally, the clear vesicle lying in each instance against the membrane of the nucleus in the last two plates has been provisionally interpreted as the centrosphere (of which there is now only one, the other having been expelled with the second polar body), undergoing a state of resorption.

8. *Other cytoplasmic inclusions.* These include vacuoles of various sizes often exhibiting a darkly stained granule within, and evidently containing some fluid secretion. There is evidence to suggest that some of these are making their way through the cytoplasm towards the perivitelline space, there to discharge their contents. Darkly stained isolated granules are occasionally met with.

9. The nucleus ranges in size from 0·020 × 0·017 to 0·030 × 0·024 mm. It has been seen quiescent, more or less central, and surrounded by a cell membrane, in Plates XI and XII (figs. 12, 13, 14). It has been observed in an excentric position and apparently devoid of a membrane (figs. 5, 6), it has also been noted more or less central and membraneless (fig. 2).

These different positions and conditions are associated with various of the stages connected with the formation of the polar bodies. The nuclear contents have been seen to include chromatin granules, isolated, paired, massed in groups, or arranged in filamentous threads. In one instance the chromatin appears in the form of a definite, thick, rod-shaped chromosome (fig. 14).

10. *The nucleolus.* A clearly defined nucleolus, displaying evidence of internal structure, is exhibited in fig. 12, which represents the condition of the mature oocyte in which the nucleus displays the characters associated with a resting stage.

In fig. 5, representing the egg at a stage corresponding to that of the extrusion of the second polar body, there is in the nuclear mass a rounded, deeply stained body, which resembles in its mass and appearance a nucleolus; what the significance of this structure is, is doubtful. Within the nuclear mass of the same oocyte there are two or three deeply stained granules which from their size might be dignified by the name of nucleoli.

11. The karyoplasm (nuclear protoplasm) has retracted from the surrounding cytoplasm in figs. 1 and 5 and from the nuclear membrane in figs. 11 and 14, so as to leave a space. Whether this be due to an artefact or is a vital process is a moot point—if the latter, its contents are probably of the nature of karyolymph or nuclear juice.

In all instances, the karyoplasm is paler and more finely granular than the surrounding cytoplasm.

In fig. 15 the karyoplasm seems to be occupied by four little clearer vesicles, each with darker stained granules around its circumference.

12. The Polar Bodies. *The First Polar Body.* What is assumed to be the *first* polar body immediately after its expulsion into the perivitelline space, is shown in fig. 3. What, there is justifiable reason for believing, is the first polar body undergoing division (coincident with the extrusion of the second polar body) is seen in figs. 8 and 9. In figs. 10 and 17 the first polar body, now divided, so that there are two, is shown in conjunction with the second polar body, now extruded into the perivitelline space, though not necessarily occupying the same position.

The Second Polar Body. The second polar body, in process of expulsion from the nuclear mass, is shown in fig. 7. Here what is assumed to be the daughter centrosphere connected with it, recognised as the dumb-bell shaped small clearer vesicular mass abutting against the inner wall of the egg envelope (see p. 187), is also evident.

The second polar body has been identified, in what are assumed to be mature oocytes owing to the nuclei having resumed a more or less central position and each having associated with it a nuclear membrane, in figs. 11 and 18, in each of which oocytes the divided first polar bodies have each been located as seen in figs. 10 and 17.

If these observations be admitted, there is distinct evidence that in man the expulsion of both polar bodies takes place before the oocyte has left the Graafian follicle, in other words, that the maturation of the oocyte with its female pronucleus is complete before it has been subjected to the influence of the spermatozoon. This is contrary to the general rule as applicable to Vertebrates, according to which, as stated by Jenkinson, "It is a rule for the sperm to enter during the second maturation division of the ovum[1]." But it may possibly be explained by the fact that in the human female congress with the male is not limited, as it is in most other mammals, to the period of "heat." In the human female, ovulation appears to take place at any

[1] *Vertebrate Embryology*, Oxford, 1913, p. 86.

stage of the menstrual cycle, whereas in lower animals as a rule it occurs in association with the condition known as oestrus or "heat." We are, therefore, justified in assuming that in our own species, the greater licence conferred upon us as to sexual union, has led to a modification of the processes involved in the maturation of the egg. An observation worthy of note in this connection is that of Heape[1], who draws attention to the fact that "in spite of the regular recurrence of the oestrus, monkeys have only a limited season during which conception is possible....this is due to the fact that the ovary is not active all the year round," which of course under the existing conditions of higher civilisation is not applicable to the human female.

A further point regarding the position of the polar bodies in relation to the axis of the egg is interesting. The evidence in the present series of observations seems to point to the fact that the point of extrusion of the first polar body through the cytoplasm need not necessarily bear any relation to the "polar" position which it subsequently assumes, but that that may be determined by the influence of gravity as it lies within the fluid occupying the perivitelline space (see p. 179). Nor is there any evidence to prove that the point of extrusion of the second polar body from the cytoplasm corresponds to that of the exit therefrom of the first polar body—the evidence, as has been pointed out (pp. 189, 203), enables us to decide that at the time of its extrusion the second polar body may occupy a position very different from that in which we see the first polar body, or its divisions, though it must be clearly borne in mind that this does not exclude the possibility of the two polar bodies having been extruded from the same site, since meanwhile, in the interval between the two extrusions, the first polar body may have altered its position by sinking to the most dependent part of the egg envelope within the perivitelline space.

The prophase condition in the formation of the first polar body is seen in figs. 1 and 2.

The anaphase condition of the formation of the first polar body is seen in fig. 3.

The metaphase condition of the formation of the second polar body is represented in Plate X and fig. 7.

Whilst the end of the telophase condition of the formation of the second polar body is exemplified in Plates XI and XII and figs. 11 and 12, and 14 and 16.

[1] "The 'Sexual Season' of Mammals." *Quarterly Journal of Microscopical Science*, New Series XLIV. 1900–1, p. 58.

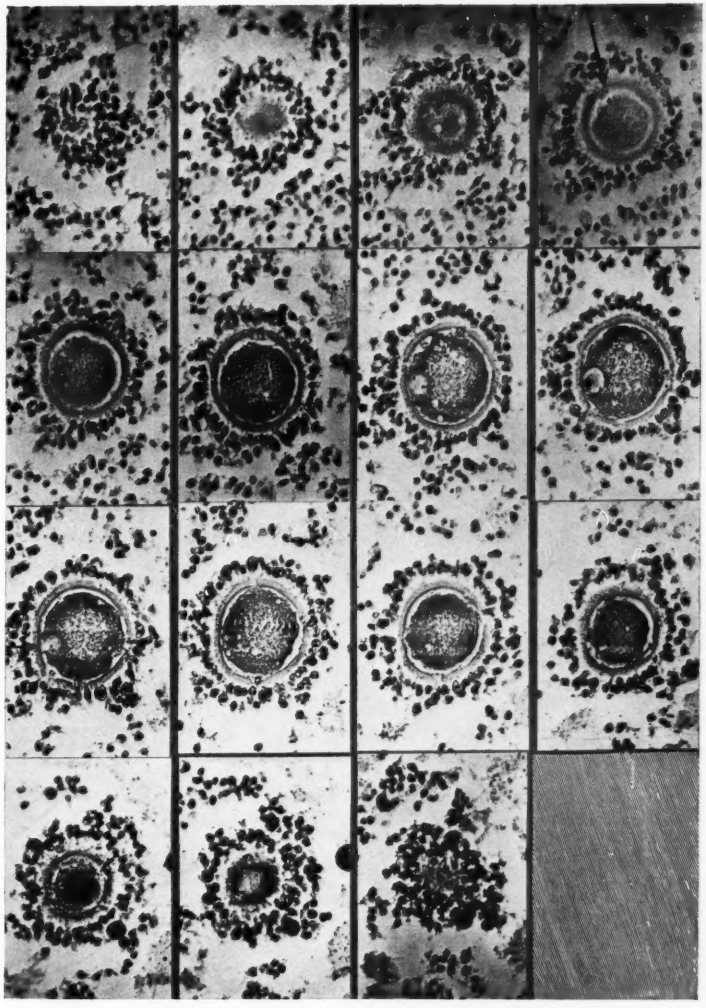

Plate X. Reproduction of complete series of sections of a human ovum in the discus proligerus (No. 453, Series A) exhibiting the extrusion of the second polar body, indicated by an arrow to the left side of the first section in the third row. The arrow in the fourth section of the first row points to the first polar body. × 150 (reduced from the photomicrographs taken with a magnification of 600 diameters).

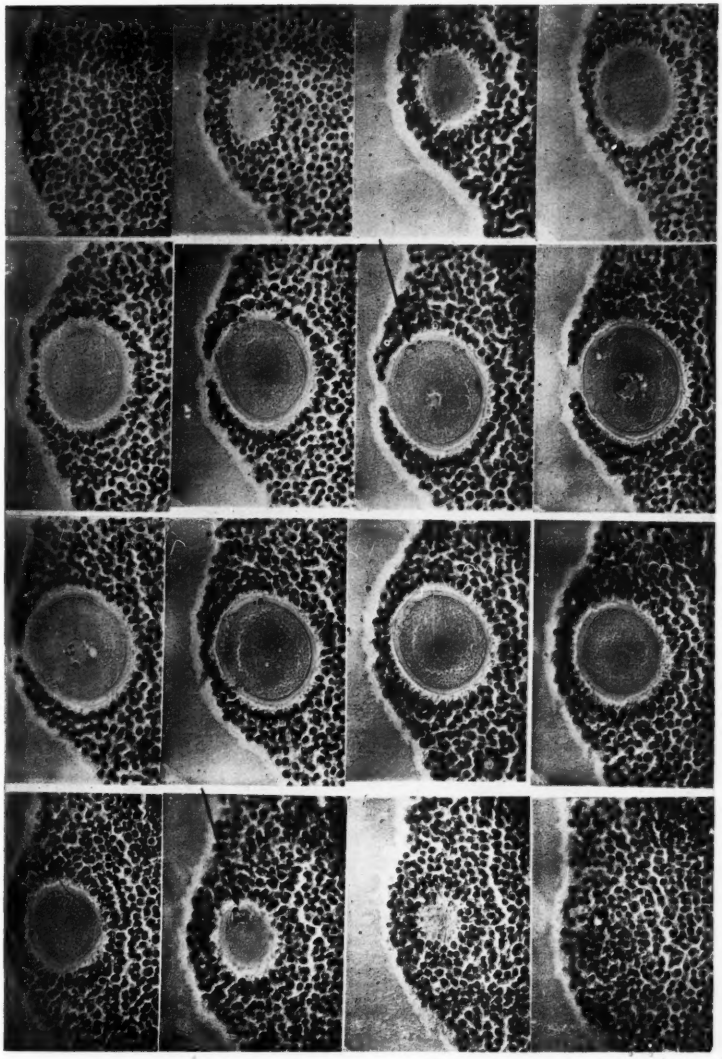

Plate XI. Reproduction of a complete series of sections of a *mature* human ovum in the discus proligerus (No. 453, Series A). The arrows in the plate point to the polar bodies: the lower to the now divided first polar body, the upper to the second polar body. Magnification 150 diameters.

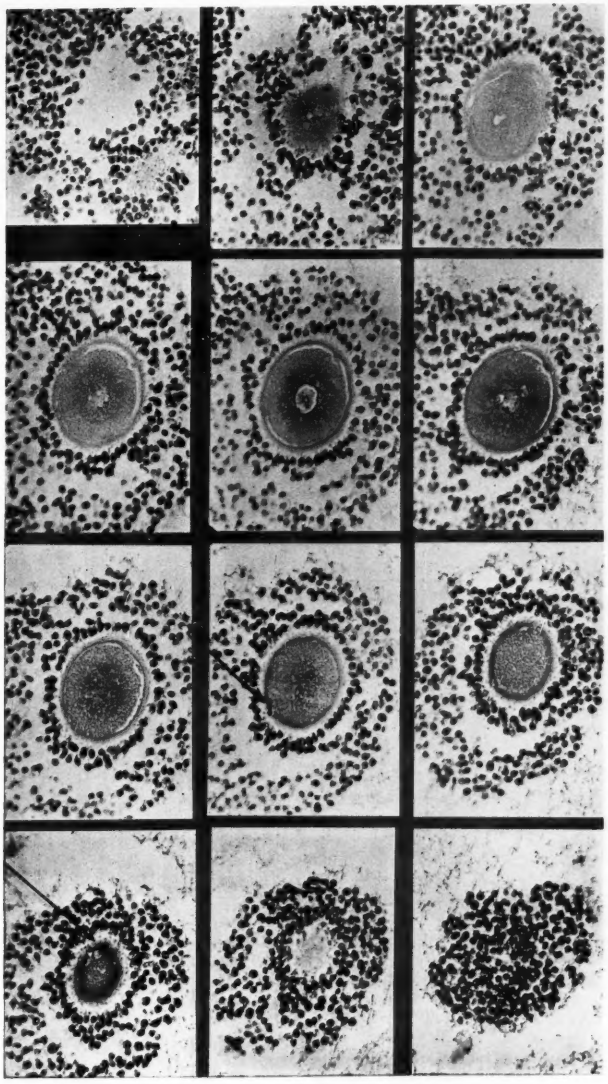

Plate XII. Reproduction of a complete series of sections through a *mature* human ovum. The lower arrow points to the divided first polar body, the upper arrow indicates the position of the second polar body. Magnification 150 diameters.

THE HOMOLOGIES OF THE ALISPHENOIDS OF THE SAUROPSIDA

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In a work still in press (Allis, in press), but of which the general summary has just been published (Allis, '18), I came to the conclusion that there apparently is, in the Reptilia, no trigemino-facialis recess, the lateral wall of the neurocranium being the primitive cranial wall; that, in the Mammalia, there is such a recess, formed by the cava epiptericum and supracochleare; and that the ala temporalis is peculiar to mammals, and is a bar of cartilage formed between the nervi maxillaris and mandibularis trigemini as they issue from the trigemino-facialis recess. In this work the only ones of the Sauropsida that were considered were Lacerta and Crocodilus, other members of the group not being taken into consideration because of Gaupp's statement ('02, p. 186) that the ground plan of the relations of the eye-muscle nerves and the trigeminus to the chondrocranium is the same in all of them. This statement by this eminent author led me to consider the trigeminus ganglion to lie, in all of the Sauropsida, external to the cranial wall, as it actually does in Lacerta and Crocodilus, and the general conclusions above referred to were based on that assumption. I was therefore greatly surprised to see, in a recent work by Kesteven ('18), that the trigeminus ganglion lies inside the cranial cavity in the Ophidia, and "on the floor of the temporal fossa" in birds. I have accordingly been led to reconsider the conditions in this entire group.

In a 25 mm. embryo of *Crocodilus johnsoni*, the alisphenoid cartilage is said by Kesteven to form the anterior boundary of a foramen prooticum, and to be attached anteriorly to the hind edge of a membrane that fills the interval between it and the orbitosphenoid cartilage. This membrane is considered by Kesteven to be a membrana spheno-obturatoria, but, because of its relations to the nerves and blood vessels of the region, I consider it to be a part of the primary wall of the cranial cavity, and not, as is the membrane of Echidna to which Gaupp ('08) first gave this name, a part of the secondary wall. The trigeminus ganglion of Crocodilus is said by Kesteven to lie upon the outer surface of this alisphenoid cartilage and so-called membrana spheno-obturatoria, and when, in a 40 mm. embryo, the cartilage and part of the membrane have ossified as the alisphenoid bone, the ganglion lies in a fossa on its external surface, and the first branch of the nervus trigeminus (nervus ophthalmicus profundus) runs forward in a groove on the external surface of the bone. This alisphenoid bone is said to articulate posteriorly with the prootic, both dorsal and ventral to the foramen prooticum, thus forming the dorsal, ventral

and anterior boundaries of that foramen, but not its posterior boundary. Ventrally, the alisphenoid articulates with the postclinoid eminence of the basisphenoid, and gives articulation externally to both the pterygoid bone and the quadrate. Dorsal to the foramen prooticum it is said to again give articulation to the quadrate. The relations of the vena capitis lateralis to the cranial wall are not given by Kesteven, but Shiino ('14) says that that vein arises in the orbit, runs posteriorly along the lateral surface of the trabecula, passes beneath the trigeminus ganglion, and then onward between the otic capsule and the quadrate; thus certainly traversing, in these early embryos, the space bridged by the quadrate between its two articulations with the alisphenoid, and hence lying external both to the latter bone and to the membrana spheno-obturatoria of Kesteven's descriptions. In later stages, some portion of that part of this vein that lies between its pretrigeminus and postfacialis portions apparently aborts, as I have shown that it does in mammals (Allis, in press), for Grosser and Brezina ('95) say that the cranial portion of the venous system of this reptile very closely resembles that of mammals. The pars ascendens of the quadrate lies between the nervi trigeminus and facialis after they have issued from the neurocranium, and hence, both in its relations to these nerves and to the vena capitis lateralis, corresponds, as I stated in my work above referred to, to the lateral wall of the trigemino-facialis chamber of fishes.

Parker, in 1883, described the alisphenoid cartilage in a series of embryos of both the crocodile and alligator, and in the earliest stages considered by him it is said to be a simple bar that rises from the lateral edge of the postclinoid wall immediately anterior to the nervus trigeminus; thus here corresponding to the conditions described by Kesteven in his 25 mm. embryo. In later stages this simple bar becomes connected with the presphenoid cartilage by a second bar, and the space between the two bars is said to be traversed by "the lesser preauditory cranial nerves." Shiino ('14) describes these same two bars of cartilage in an embryo of *Crocodilus biporcatus*, and calls them, respectively, the pila prootica and pila metoptica. The nervi oculomotorius, trochlearis and abducens leave the cranial cavity between these two bars, the trochlearis separated from the other two nerves by enveloping growth of cartilage, and hence issuing through an independent foramen. In the oldest embryo figured by Parker, the alisphenoid cartilage of earlier embryos has begun to ossify, but it is the pila prootica, alone, that ossifies, the pila metoptica remaining cartilaginous. Whether or not this latter pila is retained in the adult, either as cartilage or as bone, or is wholly resorbed, I cannot determine from the descriptions.

The first branch of the nervus trigeminus (nervus ophthalmicus profundus), which, in early embryos of the crocodile, runs forward external to the alisphenoid cartilage or bone, is said by Kesteven to later become enclosed within that bone by the formation of a lamina of bone external to it, the nerve then tunnelling the bone for more than half its width. According to Hoffman

('90) the nerve even tunnels the bone throughout its entire width, for he says that the anterior edge of the alisphenoid (his unpaired presphenoid) forms the posterior boundary of a foramen which transmits the nervi opticus, oculomotorius, trochlearis and abducens, and also the first branch of the trigeminus, from the cranial cavity to the orbit. The first branch of the trigeminus does not, however, always become enclosed in a definite canal in the alisphenoid, for Miall says (quoted by Gaupp, '02, p. 177) that, in a specimen examined by him, a splinter of bone arched over an oval slit in the wall of the alisphenoid, and the first branch of the trigeminus passed through this slit, beneath the splinter of bone.

The lamina, or splinter, of bone that thus wholly, or partially, encloses the first branch of the trigeminus of the adult crocodile apparently has its homologue in the bar of bone that, in the adults of Scomber and the Mail-cheeked fishes, separates the foramina by which the truncus ciliaris profundi and the nervus trigeminus issue from the trigemino-facialis recess, that recess lying on the internal surface of the anterior portion of the prootic and lodging the lateralis and communis components of the trigemino-facialis complex (Allis, '09). This bar of bone forms part of the lateral wall of the recess, and if the related portion of the mesial wall of the recess were to ossify, the truncus ciliaris profundi, which represents the so-called first branch of the trigeminus of reptiles, would be enclosed in a canal in the lateral wall of the cranium that would have exactly the position of the canal in Crocodilus, but that would lie in the prootic instead of in the alisphenoid. This difference in the enclosing bone is not however of importance, for any one of several bones may invade this region, as will be later explained. The vena capitis lateralis certainly lies external to this lamina of bone, for Shiino shows it ('14, fig. 8, p. 293) lying considerably ventral to the first branch of the trigeminus, between the pterygoid process of the quadrate and the processus basitrabecularis. The short so-called ascending process of the pterygoid process of the quadrate is, as Parker and Shiino both say, an epipterygoid, for the vena capitis lateralis and the first branch of the trigeminus (nervus ophthalmicus profundus) both lie mesial to it, as they normally should, and the ramus mandibularis trigemini runs outward posterior and lateral to it. The relations of the ramus maxillaris trigemini to the process are not given by Shiino, but his descriptions and figures leave little doubt that that nerve runs forward, as it should, morphologically, if not actually, lateral to the process.

In embryos of Lacerta the alisphenoid cartilage, as described by both Parker ('80 *a*) and Gaupp ('00), is similar to that of the crocodile, but without the lamina of bone (or cartilage) that forms the lateral wall of the canal for the first branch of the trigeminus. The alisphenoid of this reptile is thus simply a part of the primitive cranial wall, as Kesteven has stated; and it further differs from the bone of the crocodile in that it is, as described by Parker, an ossification of the pila metoptica, instead of the pila prootica, the latter pila

persisting as cartilage even in the adult. There is thus in this reptile, as in Crocodilus, no trigemino-facialis recess, even the small part of that recess that is represented, in Crocodilus, in the canal for the first branch of the trigeminus, being wholly wanting in Lacerta.

In Hatteria, the otosphenoidal cartilage of Howes and Swinnerton's ('01) descriptions of early embryos is later replaced by two bars of cartilage which correspond, in their relations to the cranial nerves, to the pila prootica and pila metoptica of Lacerta. The part that corresponds to the pila prootica is considered by Schauinsland ('00) to, alone, represent the alisphenoid, the pila metoptica being an orbitosphenoid. The relations of the vena capitis lateralis to these cartilages I do not find described, but sectional views given by Howes and Swinnerton show, quite unquestionably, that it runs posteriorly external to the cranial wall, between that wall and the epipterygoid and quadrate. Howes and Swinnerton say that a vein, which they call the jugular vein, traverses the basal portion of the tall fenestra enclosed between the two bars of alisphenoid cartilage, but this so-called jugular vein must be the pituitary vein of my descriptions of fishes, and not the jugular vein, which latter vein is formed in part by the vena capitis media and in part by the vena capitis lateralis. The conditions in this reptile are thus quite certainly similar to those in Lacerta.

In early embryos of *Chelone viridis* there is, according to Parker ('80 *b*), an alisphenoid cartilage which rises from the lateral edge of the postclinoid wall anterior to the nervus trigeminus. In later stages a descending process of the parietal is developed in this alisphenoid region, this process lying slightly external to the alisphenoid cartilage and forming what Parker calls the peculiarly Chelonian wall to the alisphenoid region. Concomitantly with the development of this process of the parietal, the alisphenoid cartilage is said to be almost completely resorbed, a remnant only of it persisting as a small crest of cartilage along the anterior edge of the otic capsule, dorsal to the foramen prooticum. The ventral end of the descending process of the parietal rests upon the processus epipterygoideus and the pterygoid bone, and Gaupp ('02) says that it lies external to the trigeminus ganglion, that ganglion thus being enclosed in a chamber that lies between this process of the parietal and the primitive cranial wall. The first branch of the trigeminus, and the nervus abducens, both run forward internal to this process of the parietal, the second and third branches of the trigeminus running outward posterior to it. The vena capitis lateralis lies internal to the epipterygoid, and hence internal also to the process of the parietal, this latter process thus corresponding, in its relations to this vein and the nervus trigeminus, to some portion of the pedicel of the alisphenoid of Amia. There is no trigemino-facialis recess in this reptile.

In *Chelone midas*, the alisphenoid wall apparently does not chondrify at all, for Kesteven says that the true cranial wall is formed entirely by a membrane which is attached below to the processus anterior inferior prootici and

to the postclinoid process, and from there extends upward and outward, mesial to the trigeminus ganglion, and is attached to the descending process (alisphenoidal lamina, Kesteven) of the parietal, well above the trigeminus ganglion.

In embryos of *Emys lutaria*, Kunkel ('11, '12) describes a pila prootica which is said to lie between the root of the trigeminus (des gesamten Trigeminus) posteriorly and the nervi oculomotorius and trochlearis anteriorly, this alisphenoid cartilage thus being similar to the one described by Parker in *Chelone viridis*. In front of this cartilage, the basis cranii is said to project laterally, on either side of the hypophysial fossa, and to there form a slight ridge which Kunkel considers to be a rudimentary processus basipterygoideus. The trigeminus ganglion lies dorsal to this ridge, and hence antero-lateral to the alisphenoid cartilage, that cartilage thus being, as Kunkel says, the homologue of the pila prootica of Lacerta, and hence a part of the primitive cranial wall. Kunkel describes, as a peculiarity of the specimen modelled by him, a short cylindrical rod-like process which projects postero-laterally from the internal surface of the alisphenoid cartilage; but as it was not found in any other of the specimens examined by him, and is not shown in Fuchs's figures ('10, figs. 18–19) of transverse sections through this region of this same reptile, it would seem to be an irregularity of some kind. Kunkel describes a processus ascendens palatoquadrati, and says that it is the homologue of the columella of the kionocraniate lizards. In the adult it is said to be greatly reduced, and replaced by the very variable epipterygoideum. Fuchs, in the figures above referred to, shows this same process, and there calls it the processus epipterygoideus; and as it supports, on its dorsal end, the ventral end of the processus descendens of the parietal, the conditions here are similar to those above described in Chelone.

In the Ophidia, the trigeminus ganglion is said by Kesteven to lie "inside the cranial cavity, the first branch (of the trigeminus) leaving the cranium by a veritable foramen rotundum, which is distinct from the foramen prooticum, here a true foramen ovale." The conditions in *Python spilates* are here particularly referred to, and, as stated in the second paragraph of this article, it is this statement regarding this snake that has led me to reconsider the whole group of the Sauropsida. Python I do not find particularly described in the literature at my disposal, but Hoffman ('90) says that the cranium of this snake differs only in minor details from that of Tropidonotus.

In early embryos of *Tropidonotus natrix*, Parker ('78) describes a large rounded notch between the otic capsule and "the narrow anterior part of the investing mass." This notch is said to be closed by membrane, and the trigeminus and facialis ganglia are said to lie "over" this membrane, which, as the further descriptions show, must mean external to it. Partly occluding the notch there is a wholly independent, ear-shaped flap of cartilage which Parker considers to be the alisphenoid. It lies external to the trigeminus ganglion and directly above the first and second branches of the nervus

trigeminus. In Parker's fourth stage, this alisphenoid cartilage is said to be "applied by its dilated ends to the basal plate," and it now straddles the first and second branches of the trigeminus and separates them from the third branch of that nerve, which latter branch runs outward posterior to the alisphenoid cartilage, between it and the anterior edge of the otic capsule. In Parker's sixth stage this alisphenoid cartilage, now completely ossified, has completely fused with the prootic, and the two openings between it and the prootic, one on either side of the alisphenoid, are said by Parker to be similar to the foramen ovale and foramen rotundum of human anatomy, the foramen rotundum however here transmitting both the first and second branches of the trigeminus. In one of Parker's figures of this stage (*l.c.* fig. 3, Pl. 31) the prootic would seem to have ossified in such a manner as not only to completely surround the entire root of the trigeminus, but to also separate two parts of that root one from the other, one of these parts being said to represent the third branch of the trigeminus and the other the first and second branches. This is doubtless either an error in the figure, or an individual variation, for the bridge of bone that here separates the two roots of the nerve is not shown in the figures of the adult. It was however doubtless this figure that led Hoffman ('90, Bd VI, p. 1410) to say that the prootic of this snake is perforated by three foramina, one for the nervus facialis, and the other two for "dem vorderen und dem hinteren Ast des N. trigeminus." How the second branch of the trigeminus escapes from the cranial cavity is not indicated by him, but it undoubtedly issues with the first branch. The latter branch, after it has issued through the prootic, is said to run forward and pass through a notch in the anterior edge of the alisphenoid, this notch being bridged by a band of membranous tissue attached to the alisphenoid.

The alisphenoid cartilage of Tropidonotus thus forms the outer wall of a space that lodges the trigeminus ganglion, the inner wall of the space being formed by a membrane that represents part of the primitive cranial wall, and that is, possibly, capable of ossification between two parts of the root of the trigeminus. In the adult this space forms a deep recess on the internal surface of the prepared cranium, the opening into the recess being completely surrounded by the prootic bone, but without any bridge of bone separating the roots of the trigeminus. The alisphenoid bone, which has completely fused with the prootic, forms the outer wall of this recess, and lies between the third branch of the trigeminus posteriorly and the second and first branches anteriorly. The vena capitis lateralis is neither described by Parker nor shown in any of his figures, but it certainly does not traverse the recess, for Grosser and Brezina ('95) say that, in embryos, this vein is extracranial in position, and that, in the adult, it is covered externally only by the quadrate and certain muscles. There is no indication of an epipterygoid, either as an independent cartilage or as a process of the quadrate. The quadrate apparently articulates, in the earliest stages shown, with the cranial wall, but it later becomes separated from that wall by the interposition of the dermal squamosal,

to which bone it is said by Parker to become fixed. The recess which, in this reptile, lodges the trigeminus ganglion, is thus a trigeminus recess strictly comparable to the trigeminus portion of the trigemino-facialis recess of the Teleostei, excepting in that a bar of cartilage has been formed between the second and third branches of the trigeminus, as they issue from it, instead of between the first and second branches.

Gaupp says ('02, p. 179) that he finds, in embryos of Tropidonotus examined by him, conditions somewhat different from those described by Parker. According to him no cartilage whatever is developed, at any stage, in the posterior half of the orbital region, the cranial wall there being represented by an especially dense connective tissue which corresponds strictly, in position, to the primitive cranial wall of other reptiles. The trigeminus ganglion lies in an incisura prootica in the anterior edge of the otic capsule, and is bounded anteriorly by the dense connective tissue above referred to, the three branches of the trigeminus thus traversing the cranial wall through a single foramen. In the adult he finds (*l.c.* p. 185) this single foramen divided into two parts by the formation of a bar across it, and while he does not say that this separating bar represents the alisphenoid of Parker's descriptions, it is evident that it must, differing from it only in the manner and time of its development. The third branch of the trigeminus is said to issue through the posterior one of these two parts of the single primitive opening, and the second branch through the anterior one, both nerves evidently running outward posterior to the large pars descendens of the parietal. It is not said that the first branch of the trigeminus issues with the second branch, but it evidently must, for it is said that this branch runs forward close against the membranous primitive cranial wall, in a space that lies between that wall and the pars descendens of the parietal, there being accompanied by the nervi oculomotorius, trochlearis and abducens, and also by the nervus opticus. All of these several nerves then issue into the orbit through a large opening between the parietal and frontal, which Gaupp calls the foramen orbitale magnum. It is not said that the vena capitis lateralis traverses this same foramen and then runs posteriorly internal to the pars descendens of the parietal, but such must evidently be the case. The pars descendens of the parietal thus here occupies the position, relative to this vein and the several cranial nerves, both of the corresponding process of the parietal of Chelone and of the pedicel of the alisphenoid of Amia, and hence is quite unquestionably an ossification of tissues that represent the epipterygoid, which element is, as just above stated, otherwise wholly wanting in this reptile.

In *Vipera aspis*, Peyer ('12) finds a bone which he refers to as the so-called alisphenoid, but he says that it is probably simply a part of the prootic. It is said to be a primary, or substituent, bone, but not preformed in cartilage, and Peyer apparently considers it to form a part of the primitive cranial wall. Its relations to the second and third branches of the trigeminus are not given, but as it is said to lie lateral to the trigeminus ganglion, and is referred to as

the alisphenoid of Parker's descriptions, it must be the homologue of that element, and hence not a part of the primitive cranial wall. A horizontal slit separates the anterior portion of the bone from the basal cartilage, and it would seem as if it must give passage to a pituitary vein.

In the Aves, Kesteven says that the trigeminus ganglion "appears to lie on the floor of the temporal fossa on the alisphenoid in front of the petrosal, with the foramen rotundum very close to the foramen ovale, and the first branch (of the trigeminus) passing forward through the bone, not upon it." Nothing is said as to the veins, but it is probable that if an important vein had traversed the so-called temporal fossa and issued through either of the foramina mentioned, it would have been so stated. That this vein does not traverse the fossa is also apparent from Gadow's ('91) descriptions of the veins in the adult bird, for he says that the venae faciales externa and interna unite to form a vena facialis communis which falls into the vena cephalica communis s. jugularis, and no one of these several veins is said to traverse any part of the cranial cavity. The venae faciales communes of opposite sides are said to be connected by cross-commissure, and this cross-commissure would seem to represent the pituitary veins of my descriptions of fishes were it not that it apparently, as shown in the figures given, lies external to the cranium. In any event, the vena facialis communis would seem to correspond to the jugular vein of my descriptions of fishes, and it quite certainly does not traverse the temporal fossa, that fossa thus apparently being, as is the corresponding fossa in Tropidonotus, the trigeminus portion of a trigemino-facialis recess.

Parker ('69) says that, in early embryos of the chick, the alisphenoid cartilage forms the anterior border of a large foramen ovale, and that it is itself perforated by a foramen rotundum. When this alisphenoid cartilage ossifies, the ossification proceeds from two centres, one lying between the two above mentioned foramina, and the other anterior to the anterior foramen. In older embryos, only one of these two foramina is described or figured, and it has the position of the posterior one of the two above mentioned ones. What has become of the other foramen is not indicated.

Tonkoff ('00) and Gaupp ('02, '05) both also describe the cranium in certain early stages of the chick, and they both differ from Parker in that they find but a single trigeminus foramen. A cartilage is described, by both of them, that corresponds to Parker's alisphenoid cartilage, but it is called by Gaupp the sphenolateral plate. It is said to arise from the basal plate of the cranium as a pillar of cartilage that lies between the second and third branches of the trigeminus posteriorly, and the first branch of that nerve anteriorly, and to have two portions which lie nearly at right angles to each other, an anterior one looking forward, toward the orbit, and a posterior one looking laterally. The sharp edge between the two portions of this cartilage is said to form the so-called postorbital process. The single large foramen that transmits the second and third branches of the trigeminus lies between the

posterior portion of the cartilage and the anterior edge of the otic capsule, and it is said by Gaupp to be a typical foramen prooticum, notwithstanding that it is not traversed by the first branch of the trigeminus. According to Cords ('04) the second and third branches of the trigeminus, as they issue through this foramen, may be separated from each other by a pillar of bone. The anterior portion of the alisphenoid plate is largely fenestrated, but this fenestra is closed by membrane and not traversed by any structure. In later stages the membrane ossifies as part of the alisphenoid bone, without having previously undergone chondrification. Anterior to and continuous with the base of the alisphenoid cartilage, there is a plate of cartilage which rises from the trabecula in the hypophysial region, and it is perforated by foramina for the nervus trochlearis and the arteria ophthalmica. Because of its perforation by these two foramina, this plate must form part of the primitive cranial wall.

Gaupp says that, in Tinnunculus, but not in the chick, a dorso-lateral portion of the foramen prooticum is cut off by a bridge of cartilage to form a separate foramen which is traversed by a vein. No intimation is given as to what this vein may be, but it would seem as if it must be a vein that corresponds to the vena cerebralis anterior of Grosser and Brezina's ('95) descriptions of Tropidonotus, that vein of that reptile issuing from the cranial cavity in the region of the trigeminus foramen and falling into the vena capitis lateralis. I do not find the latter vein described in early stages of the chick, but it must certainly lie external to the cranial wall, as it does in all of the Reptilia.

The trigeminus ganglion of the chick thus lies in a trigeminus recess similar to that of Tropidonotus excepting in that the base of the alisphenoid cartilage lies between the first and second branches of the trigeminus instead of between the second and third branches of that nerve; but a bar of cartilage, or bone, is sometimes formed, as it is in Tropidonotus, between the second and third branches.

From the above descriptions it is evident that there are two actual, or potential, walls in the alisphenoidal region of the neurocranium of the Sauropsida, and that these two walls correspond to the inner two of the three walls described by me in this region of fishes (Allis, '14 *b*). The outer one of these three walls of fishes is formed by cartilage, or bone, that corresponds to the otic process of the palato-quadrate of amphibians, and hence is not a part of the primordial neurocranium. The other two walls apparently both form parts of that neurocranium, but the inner one, only, forms the primary bounding wall of the cavum cerebrale cranii. The outer one of these two walls is apparently a serial homologue of the outer wall of the otic capsule, and, like that wall, it would acquire bounding relations to the cranial cavity if the inner wall were to be suppressed; and if certain parts of it should then undergo chondrification or ossification, while other parts persisted as membrane, the several arrangements above described in the Sauropsida would

all arise. This is all so well illustrated by the conditions actually found in Bdellostoma, that they may here be briefly resumed.

The trigemino-facialis ganglion of Bdellostoma lies in a cavity in the membranous cranial wall that is apparently strictly similar to the trigemino-facialis recess of fishes, excepting in that it lodges the entire ganglionic complex instead of only its communis and lateralis components. I formerly (Allis, '03) considered this cavity to be a trigemino-facialis chamber similar to that of Amia, but I now recognise that it is a trigemino-facialis recess, or pars ganglionaris of a trigemino-facialis chamber, and not a complete chamber, for the veins that drain the orbit and the mandible, and hence correspond to the jugular vein of the gnathostome fishes, both lie external to the recess. The inner wall of the recess forms the bounding wall of the cavum cerebrale cranii, its outer wall corresponding to the membrana sphenoobturatoria of Gaupp's descriptions of Echidna. The recess is incompletely separated into trigeminus and facialis portions, and the four apparent roots of the trigemino-facialis complex perforate its inner wall by more or less distinctly separate foramina. The branches of the complex then leave the recess by five foramina: an anterior one for the ramus ophthalmicus, an antero-ventral one for the ramus palatinus, a ventral one for the ramus maxillo-mandibularis, a lateral one for the ramus buccalis, and a postero-ventral one for the nervus facialis.

There are thus several membranous pillars between the several nerves that issue through the outer wall of the trigemino-facialis recess of Bdellostoma, and as these pillars do not differ, in composition, from other portions of the cranial wall, it is evident that each one of them is as capable either of persisting as membrane, or of undergoing either chondrification or ossification, as are those other portions of the cranial wall. Assume that a similar pillar is formed between the rami maxillaris and mandibularis trigemini. If then, in a primitive fish in which the conditions were as would then here be found in Bdellostoma, that part of the cranial wall that corresponds to the pila prootica of the gnathostome fishes were to chondrify, the inner and outer walls of the trigemino-facialis recess persisting as membranes, the conditions actually found in Lacerta would arise. If the alisphenoid cartilage, thus developed, were to ossify, and that part of the outer wall of the recess that lies between the first and second branches of the trigeminus were to be prolonged anteriorly so as to slightly overlap the alisphenoid, and were then to ossify without previous chondrification, it would give rise to the conditions found in Crocodilus; while if that part of the outer wall that lies between the second and third branches of the trigeminus were to chondrify, or ossify, instead of the part that lies between the first and second branches of that nerve, it would give the conditions found in Tropidonotus. If neither the alisphenoid nor any part of the outer wall of the trigemino-facialis recess were to chondrify, but extracranial tissues that represent the epipterygoid were to ossify as the processus descendens of the parietal, the conditions in *Chelone midas* would arise;

while if, in addition to this, the alisphenoid cartilage were to develop and then later be almost completely resorbed, it would give the conditions in *Chelone viridis*. If the basal portion of the pila prootica, the part that lies directly in front of the nervus trigeminus, did not develop, and that part of the outer wall of the trigemino-facialis recess that lies between the first and second branches of the trigeminus were to chondrify, the conditions described by Tonkoff and Gaupp in the chick would arise; while if, in addition to this, the tissues between the second and third branches of the trigeminus were to chondrify, or ossify, it would give the conditions described by Parker and Cords.

It is thus seen that the alisphenoids of the Sauropsida are not homologous structures, as Kesteven ('18) concludes, excepting in the sense that they are all chondrifications, or ossifications, of membranous tissues that lie, in part, between the trigeminus and the more anterior cranial nerves, and in part form the inner and outer walls of the trigeminus portion of a trigemino-facialis recess. In their relations to the trigeminus ganglion, and to the several branches of the trigeminus nerve, they vary greatly, and their basal portions are not all homologous. In the Teleostei, the alisphenoid never, so far as I know, forms any part of the outer wall of the trigemino-facialis recess, that wall ossifying as part of the prootic; and the conditions here differ also from those in the Sauropsida in that a pillar of the prootic is usually found between the nervi trigeminus and facialis, but never, so far as I know, between the second and third branches of the trigeminus. In Amia, a distinctly different type of alisphenoid is found, for, as stated in an earlier work (Allis, '14 *a*), the pedicel of the alisphenoid of this fish is, like the processus descendens of the parietal of Chelone, the homologue of the ascending process of the palato-quadrate of amphibians and of the epipterygoid of reptiles, and hence not a part of the primitive cranial wall.

My conclusion (Allis, '18) that the ala temporalis is peculiar to mammals is thus incorrect, for the lamina perpendicularis of that element of the cranium is evidently strictly comparable to the bar of cartilage that, in Tropidonotus, and occasionally in the chick, lies between the second and third branches of the trigeminus. The conditions in mammals differ, however, from those in all of the Sauropsida above considered in that the alisphenoid extends posteriorly beyond the third branch of the trigeminus, and, in most mammals, occupies that portion of the lateral wall of the trigeminus recess that lies between that branch of the trigeminus and the otic capsule.

In the Marsupialia and Insectivora, some part of the posttrigeminus portion of the alisphenoid forms the so-called tympanic wing of that bone, and Kesteven considers this wing of this bone to be the homologue of the "Echidna-pterygoid." The wing is said by von Kampen ('05) to form the outer bounding wall of the tympanic cavity, and hence is not an ossification of the actual bounding wall of the trigeminus recess (cavum epiptericum). The Echidna-pterygoid, also, is apparently not primarily a part of the bounding wall of the trigeminus recess, for although, in the adult, the bone does

actually form a considerable part of the outer wall of the cavum epiptericum of the prepared skull, it is not an ossification of the membrana spheno-obturatoria, and hence not a part of the primary wall of that cavum. In embryos, the anterior part, only, of the pterygoid has relations to the cavum, that part of the bone giving attachment to the ventral edge of the membrana spheno-obturatoria and hence there forming part of the floor of the cavum. Its posterior portion has, however, no relations whatever to the cavum, lying considerably ventral to the membrana spheno-obturatoria, along the ventral surface of the pars cochlearis of the otic capsule, and even separated in large part from it by the musculus tensor tympani (Gaupp, '08, text-figs. 36 and 44). The membrana spheno-obturatoria is said by Gaupp ('08, pp. 649–650) to ossify, in large part, as the so-called alisphenoid of the adult, but this bone of the adult is said by him to contain no part of the ala temporalis of embryos, and he suggests, in explanation of this, that the ala temporalis of embryos must have been either wholly resorbed in later stages of development, or, perhaps, have been destroyed in the preparation of all of the skulls of the adult that have been used for existing descriptions. A part of the membrana spheno-obturatoria is said to ossify as the temporal wing of the palatine, and another part of it to be replaced by a portion of the squamosal, but Gaupp says that this latter bone lies external to the membrane in embryos, and hence cannot be an ossification of it. The conditions are complicated, and evidently indicate, as Gaupp says, that the inclusion of the pterygoid in the wall of the cavum epiptericum of the adult is due to the inclusion in that cavum of a space that lay external to the cavum of embryos. This probably does not apply to the squamosal, that bone apparently lying close against the membrane, without appreciable intervening space; and this would seem to also apply to those portions of the frontal and parietal that, in other mammals, may acquire bounding relations to the cavity. In Orycteropus, the orbitosphenoid cartilage is said by Parker ('85) to extend posteriorly, internal to the alisphenoid, throughout nearly half the length of the latter bone, thus here representing a chondrification of the anterior portion of the inner wall of the trigeminus recess. The walls of the recess seem, in fact, to have been a veritable battle ground for the adjacent bones, for each one of them, whether primary or dermal, excepting only the postfrontal, has, in some one of the vertebrate series, succeeded in invading them.

The processus alaris of mammals forms part of the outer wall of the trigeminus recess (cavum epiptericum). It cannot therefore be the homologue of the processus basipterygoideus of reptiles, as Kesteven concludes, and as Gaupp ('02) maintains, for the latter process lies wholly external to the trigeminus recess; and, furthermore, the relations of this process to the nerves and blood vessels of the region all indicate that it is, as stated in my recent work (Allis, '18), the homologue of the floor of the orbital opening of the myodome of Amia. If, as seems probable, the epipterygoid has been

derived from the basal portions of the posterior row of branchial rays of the premandibular arch, the processus basipterygoideus would seem to represent the pharyngo-branchial of that arch. The processus pterygoideus of mammals is, as stated in my work above referred to, a persisting remnant of the outer wall of the trigemino-facialis chamber of fishes. The great wing of the sphenoid bone of man corresponds to a part of the prootic of the Teleostei, and not to the alisphenoid. The teleostean alisphenoid and orbitosphenoid are represented, respectively, in the postopticus and preopticus portions of the small wing of the sphenoid.

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MENTON, FRANCE.
November 27, 1918.

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THE PTERYGOIDS IN AMPHIBIA AND REPTILES AND THE PARASPHENOID

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Beyond the description of the conjoint pterygoid, or parasphenoid, in the crocodiles the present contribution offers no new statement of fact; it is a further argument in support of a thesis defended in a previous article published in this paper. It was intended to withhold any extended defence of that thesis until a more complete survey of the literature would enable me to include a résumé of such embryological works as bear upon the subject.

My recent discovery of the long-standing error included in all descriptions of the palatal aspect of the crocodilian skulls justifies the present publication.

The thesis referred to is as follows:

(1) The greater part of the parasphenoid of the Amphibia is represented in super amphibia by the paired pterygoids.

(2) The amphibian pterygoid appears elsewhere only in some reptiles, in which it has been termed ectopterygoid or os transversum.

(3) The reptilian parasphenoid represents the anterior portion only of the amphibian parasphenoid.

PART I

THE AMPHIBIAN PARASPHENOID AND PTERYGOIDS

There are two types of skull presented for study. These two differ in a very marked manner, Loxomma from all other forms.

The typical amphibian skull is presented in Rana and Branchiosaurus (fig. 1). The characteristic feature here is the large ⊥ shaped parasphenoid whereof the perpendicular limb lies in the midline beneath the neurocranium and extends forward to articulate with the palatines and prevomers and underlies the nasal chambers. The transverse arm, stouter and shorter, underlies the neurocranium and parotic masses behind the sella.

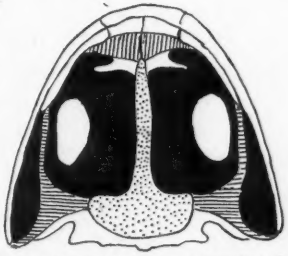


Fig. 1. Branchiosaurus. From Zittel, *Palaeontology*[1].

The pterygoid bone presents with fair constancy three arms; the first or body, stouter than either of the others, articulates with the parasphenoid below the parotic mass; the second passes forward to articulate with the maxilla, sweeping round between the

[1] Throughout the series, the parasphenoid and its derivatives have been stippled, the prevomers hatched with perpendicular lines, and the ossa transversa and amphibian pterygoids hatched with horizontal lines.

orbit in front and the muscles of the temporal fossa behind; the third arm passes back and out to give support to the suspensorium posteriorly. This pterygoid is a cranio-visceral element developed in membrane in relation to the suspensorium and maxillary arch to give rigidity thereto. Of the three components the body and anterior arm are the best developed in most forms.

In a few forms (e.g. Cryptobranchus (fig. 2), Salamandra and Amblystoma) the anterior arm fails to reach the deficient maxillary arch.

In *Ichthyophis glutinosa* (fig. 3) the pterygoid is much reduced, presenting both in situation and form the appearance of a typical reptilian os transversum.

In Loxomma (text-fig. 4) little or nothing of that disposition of these bones which we have been discussing is recognisable in the figure of Embleton and Atthey which I reproduce, and from which alone I know the skull. In the place of the median parasphenoid we find very much expanded pterygoids,

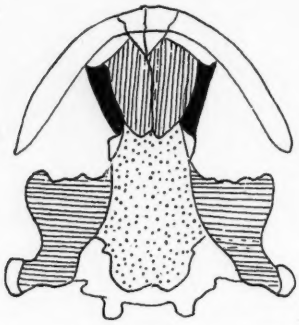


Fig. 2. Cryptobranchus. From Zittel, *Palaeontology.*

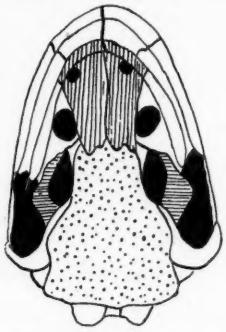


Fig. 3. Ichthyophis. From J. S. Kingsley, *Vertebrate Zoology.*

which in front extend on either side of the palate bones instead of between them, and they are so extensive as to form, each on its own side, a nearly complete floor to the orbit. An ectopterygoid is depicted occupying nearly the position of the pterygoid in Ichthyophis.

Difficulty was apparently experienced by the authors in arriving at satisfactory designations for all the bones—we find a "ridge on the median line between palate and pterygoid bones" is so named. It is noteworthy that no suture is either definitely shown or even indicated between the two pterygoids where that ridge is perfectly preserved. The basisphenoid is recognised above the choanae, which open behind the pterygoids; i.e., far back, as in the crocodiles. The floor of the choanae is left unnamed.

If it be as the drawing shows that the roof of the posterior portion of the naso-pharyngeal canal is the basisphenoid then it follows that the parasphenoid is either absent from the base of the skull in this region, or has been perforated somewhere further forward by the canals, and here lies beneath

the choanae. That the parasphenoid should be absent from the base of the skull posteriorly, is not a bold postulate, because it is so absent according to accepted views in all reptilian skulls, and this labrynthodont presents marked resemblance to the reptiles. We do not, however, find the naso-

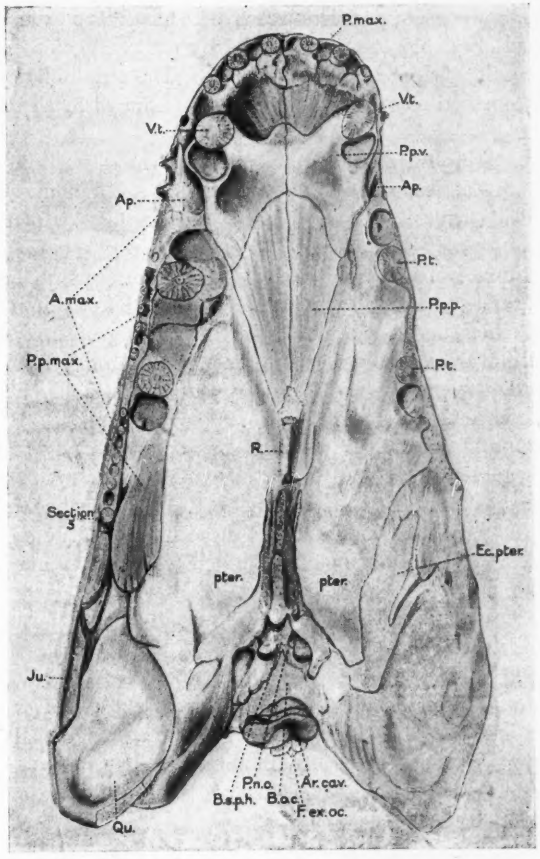


Fig. 4. Loxomma Allmanni. From Embleton and Atthey, *Ann. Mag. Nat. Hist.*, Ser 4, Vol. 14, Pl. V. $\times \frac{2}{3}$.

pharyngeal canals or choanal fossa roofed by the basisphenoid in any of the reptiles, excepting only some fossil crocodilians, and of these more anon.

The situation of the choanae in Loxomma was compared to that in the crocodile; it may be remembered that in this skull as in that of the alligator and gavial the roof of the choanal fossa and of the post-narial canals is provided by what has been termed the "pterygoids." It is probable that a

re-examination of Loxomma will show that the roof of the fossa and canals is provided by bones homologous with the pterygoids of Crocodilus.

Though the two pterygoids are not together ⊥ shaped, it still remains a fact that in Loxomma the place of the amphibian parasphenoid is occupied by paired pterygoids, and the place of the pterygoids by ossa transversa, which undeniably occupy positions relative to maxillary arch and so-called pterygoid precisely analogous to that held by the pterygoids of Ichthyophis relative to maxillary arch and parasphenoid. The amphibian parasphenoid has quite disappeared from the skull, which is, however, still to be regarded as amphibian.

The last paragraph is a concise statement of the disposition of the bones as indicated by Embleton and Atthey's drawing and not an attempted explanation of the disposition. It is also a concise history of a remarkable change.

On the evidence of published figures and descriptions, in Loxomma and all other Amphibia paired pterygoids were present; the primitive form was that of Rana since such is the most prevalent among both recent and fossil forms. In all amphibian skulls except that of Loxomma a parasphenoid is well developed, the possession of this bone may justifiably be regarded as typical, its absence as aberrant.

In Loxomma then the parasphenoid has been partially or entirely lost and the pterygoids have come to occupy a median situation replacing the parasphenoid, at the same time depriving the maxillary arch of its usual support; this so weakened the arch that a new support, the os transversum, was developed in the old place of the pterygoid. A truly remarkable process of evolution!

If there be truth in the thesis stated above, an explanation calling for less wonderment is available.

The so-called pterygoids are in reality but the two halves of a modified parasphenoid and the ossa transversa are the pterygoids. This is surely a more acceptable explanation than to assume (1) that the parasphenoid disappears, (2) the pterygoids undergo marked modification in (*a*) form, (*b*) situation and (*c*) function, and (3) a new element is developed to assume their old function and situation.

The explanation offered under my thesis involves only the assumption that the parasphenoid ossifies from two centres, if indeed the so-called pterygoids are divided by suture along that unnamed "central ridge."

Assuming the correctness of the drawing, that two bones are present, the suggestion here is that the so-called paired pterygoids of Loxomma are homologous with the unpaired parasphenoid of the generality of amphibian skulls and that the so-called ectopterygoids of the one are homologous with the pterygoids of the other.

As against this, it may be contended that we are not only asked to recognise the unpaired parasphenoid in paired elements, but also those paired

elements together do not occupy precisely the situation of the parasphenoid and are moreover separated from the base of the skull by post-narial cavities.

In reply to these objections, it may be justly argued: (1) That there is no satisfactory evidence that the pterygoids of Loxomma are paired elements, the specimen is damaged in the midline so that they may be in reality the right and left halves of a bilaterally symmetrical median bone. (2) That the matter of precise situation cannot be regarded as a weighty objection. A survey of the accompanying drawings should convince one of this for it will be seen there, that, in the different reptiles, the paired pterygoids present the most remarkable variety of shape and disposition, preserving only certain relations, yet their identity as pterygoids and homology *inter se* has not and cannot be questioned. (3) The imperfections of the Loxomma skull are such as to justify the assumption already made, that is, that there may be as in Crocodilus (*vide postea*) a portion of the so-called pterygoids between the choanal cavities and the base of the cranium.

PART II

THE CROCODILIAN SKULL

In *Crocodilus porosus* separate pterygoid bones are not present except *in ovo*, at birth the two are completely fused to form a "conjoint pterygoid." In this case my thesis has been unconsciously applied by all of us, we have been designating a veritable parasphenoid "pterygoids." In making the correction one is also in a position to state that apart from the thesis here advanced, the past practice is only justified by the fact that the bone ossifies from two centres which early fuse.

This conjoint pterygoid (figs. 5–8) lies on the base of the skull beneath the neurocranium below the basisphenoid and extends forward between the orbits nearly as far as the anterior boundary of the infra-orbital palatal vacuity.

It is most conveniently described as consisting of body, naso-vomerine and naso-palatine portions. The body (section A—B) roughly x-shaped in transverse section is applied to the under aspect of the basisphenoid, its two dorsal arms extend upward on either side of that bone to articulate with the pars subparotica of the quadrate (fig. 7). The ventral aspect of the body is the roof of the posterior portion of the naso-pharyngeal canal and of the post-narial fossa, separating these from the basisphenoid. The two ventral arms have the naso-palatine plates attached to them, and anteriorly they merge into the naso-mural component of the naso-vomerine portion of the bone.

The naso-palatine plates are the portions of the bone which in the past have been termed the pterygoids on the palatal aspect of the skull. Expanded in the palatal plane they constitute the bony palate behind the posterior transpalatine suture, meeting in the midline they there articulate with one another to form the deceptive so-called interpterygoid suture.

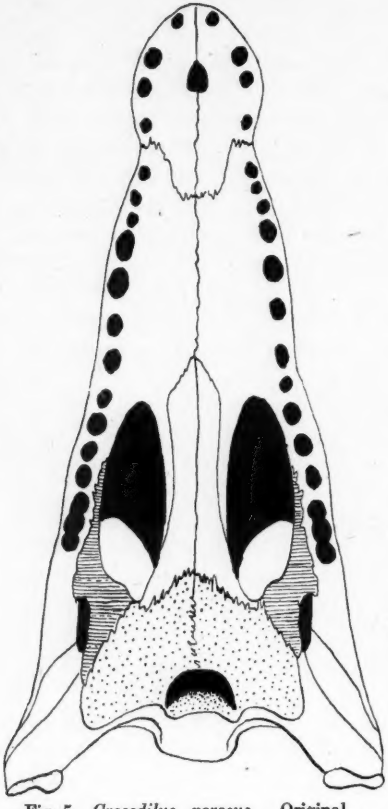


Fig. 5. *Crocodilus porosus.* Original.

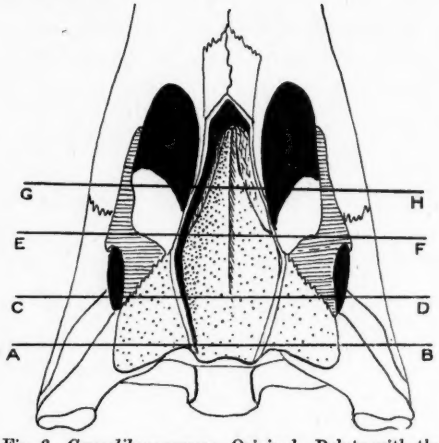


Fig. 6. *Crocodilus porosus.* Original. Palate with the palatine plates cut away below the post-narial canals. *A—B, C—D, E—F, G—H,* sections of the "pterygoid" along the lines of section indicated. The ventral surface is uppermost.

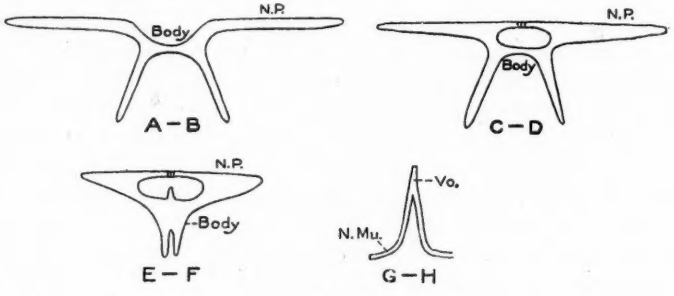


Fig. 6 *a.*

Along the posterior transpalatine suture these plates articulate each with the palatine of its side, and, just behind and lateral to this with the corresponding os transversum. On either side of the midline these plates form the floor of the post-narial canal (sections *c*—*d* and *e*—*f*). In fig. 6 the medial portion of the nasopalatine plates and portion of the palatine laminae of the palatine bones have been removed to show the extent and form of the naso-vomerine portion of the conjoint pterygoid above them. What may be termed the naso-mural components of this portion of the bone are anterior continuations of the ventral arms of the body, which in front of the naso-palatine plates articulate with the naso-mural laminae of the palatine. The suture swings across from the floor of the nasal canal posteriorly to the roof anteriorly, where these laminae are abruptly terminated (fig. 7). The vomerine portion

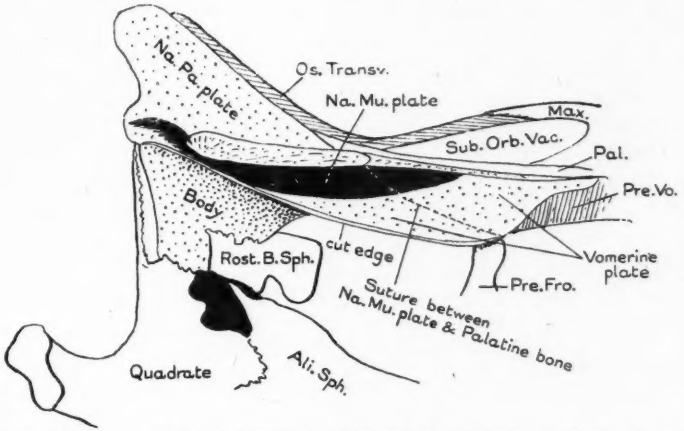


Fig. 7. *Crocodilus porosus.* Original. Side view with the near neutral arm of the body and naso-mural wall of conjoint pterygoid removed. *S.* suture between naso-mural plate and palatine bone, shown by dotted line through vomerine partition; *c.* cut edge.

(figs. 6, section G—H, and 7), commencing behind as a ridge on the ventral surface of the body becomes in front of the body gradually developed into a complete partition between the two nasal canals, the ventral edge of this partition articulates with the two palatines along the middle two fourths of the inter-palatine suture. Seen from above the vomerine portion is found to be double (section G—H); the cartilaginous int-orbital septum fills the trough in the fresh state.

Just at the anterior limit of the naso-mural component, the bone articulates with a spur from the prefrontal on each side (fig. 7) and in front of this each lamina of the vomerine portion articulates with the hinder end of the prevomer of its side.

This description is based on an exceptionally good specimen measuring

12¼ inches in length, in which none of the sutures are closed so that it was very easy to disarticulate.

In older specimens, the vomerine ridge is carried back to the posterior limit of the body, and gives the misleading appearance of a calloused closed suture.

In the skull of a young specimen (25 mm. in length) taken from the egg I find evidence of two centres of ossification, each centre was apparently situate at the junction of naso-palatine plate and ventral arm of the body, the ossifications at this stage are triradiate in cross section, one arm representing the median, a second the lateral portion of the naso-palatine plate, the third arm representing the ventral arm and median portion of the body. A fine splint runs forward from the body along the roof of the post-narial canal of its side.

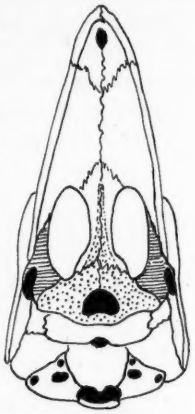


Fig. 8. *Crocodilus porosus*. Original (specimen 42 mm. long).

At a stage a little later than this (fig. 8), 40 mm. in length, the bone presents all the adult features except the dorsal arms of the body, the two centres of ossification having fused above the choanae and the naso-vomerine portion being well developed; there is no trace of suture along the middle of the body or naso-vomerine portion.

One remarks in the young skull the position of the choanae, the posterior limit of the conjoint pterygoid and expanse of basisphenoid and basioccipital exposed on the palatal aspect of the skull. These features recall the fossil crocodilians, none of which have the true basicranial bones so completely covered below by the pterygoids or the choanae situate so far back as in the adult Crocodile.

GONIOPHOLIS, TELEOSAURUS AND BELODON

In Goniopholis paired pterygoids nearly surrounding the choanae, meeting in the midline behind and above them, but not on the palatal boundary have been described. There is also a median vomerine crest formed apparently from the joined pterygoids (fig. 9). In Pelagosaurus there is a very similar condition. In Teleosaurus as figured by Zittel the roof of the post-narial fossa is designated basisphenoid, the pterygoid is not shown, and the limits of the bones designated ectopterygoid are not defined. Using the disposition of the bones in Crocodilus, Goniopholis, and Pelagosaurus as a working basis Zittel's figure is here reproduced, and the sutures "restored" (fig. 10).

Belodon, and presumably the rest of the Parasuchia, appear to be out of place among the crocodilia. The form of the pterygoids, the prevomers entering into the bony palate, the anterior situation of the choanae, the separated palate bones, the presence of postorbitals, paired parietals and frontals and the well developed abdominal ribs together with the form of the

clavicle and coracoid, indicate rhynococephalian affinities, more emphatically than the crocodilian features indicate crocodilian affinities.

This review of crocodilian skulls, brief though it be, leads to the conviction that in the true crocodilian skull there is, in place of the so-called paired pterygoids, a bilaterally symmetrical conjoint pterygoid or parasphenoid. Such is demonstrably the case in Crocodilus itself. A comparison of the three leads to the further conviction that the so-called ectopterygoids of Crocodilus are homologous with those of Loxomma and with the pterygoids of Icthyophis.

There can be little doubt that in the form and development of the bones in Crocodilus we can, as it were, recognise the past, present and future of the parasphenoid and pterygoids.

In its general development and relation to skull areas the parasphenoid is as in Branchiosaurus a roughly "⊥ shaped bone whereof the perpendicular limb lies in the midline beneath the neurocranium and extends forward to articulate with the palatines and prevomers and underlies the nasal chamber.

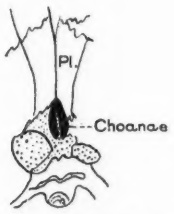


Fig. 9. Goniopholis. From Zittel, *Palaeontology*.

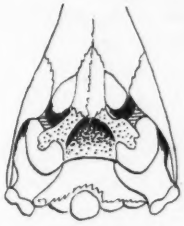


Fig. 10. Teleosaurus. From Zittel, *Palaeontology* (modified).

The transverse arm stouter and shorter underlies the neurocranium and paroccipital masses behind the sella." Though in detail this description needs modifying; for the angles between the arms have been filled in to produce a triangular bone, the otocrane is contracted to the side of the skull to the more or less complete extinction of the paroccipital mass, and the "perpendicular arm" is found above as well as below the nasal chamber; there can be no question but that in the main and in all essentials it is correct, and the bone is a parasphenoid.

Turning now to the details, we find this bone in each half to present very truly the relations of the reptilian pterygoids, more especially the primitive condition as represented in the Chelonians. If we compare for instance the two halves of the bone as represented in fig. 6 where the palatine plates have been cut away below the post-narial canals with the illustration of *Chelonia midas*, it will be found that the dispositions are very similar. As differences we note in Chelonia the presence of an independent median vomer, the absence of paired prevomers, and the lateral portions of the naso-palatine plates are applied directly to the parotic mass.

In the matter of the median vomer, its absence is entirely in accord with Broom's hypothesis that the median vomer is developed from the anterior portion of the parasphenoid, and, remembering that there is strong evidence elsewhere in support of that hypothesis, one is not surprised at the absence of median vomer in the presence of the vomerine component of the parasphenoid. The differences which may be noted cannot be allowed to weigh against the similarity especially when we remember the differences exhibited among the pterygoids of different reptilian forms, and especially in view of the fact that the similarity to the paired pterygoids is such that, up to the present, the conjoint bone has been regarded as paired pterygoids by every writer who has dealt with the skull.

The bone is therefore homologous with paired pterygoids. We have previously seen that the bone in question is also the same bone as the amphibian parasphenoid; to paraphrase our boyhood's enemy, Euclid, bones which are homologous with the same bone are homologous with one another and the paired pterygoids of the majority of the reptiles are homologous with the parasphenoid in amphibia.

It is possible that it may be objected that inasmuch as the crocodilian parasphenoid is developed from two centres it is to be regarded as paired pterygoids which have become fused by the precocious obliteration of the suture. Such an argument must, however, fail because some explanation must be sought for such precocious obliteration of this single suture.

It must be remembered that this suture becomes obliterated at a time when not only this bone but all the other membrane bones are as yet only partly developed.

In point of fact, the early independence of the two halves of the bone exhibit us its future division into "pterygoids" whilst the fusion is the result of hereditary habit is as it were past history.

Stated differently we see in Crocodilus how it is possible for a single median bone of a more primitive skull to be replaced in the process of evolution by paired bones in the more advanced skull. The first stage is the development of two centres of ossification, the second would be the failure of these to coalesce.

If, as there is now good reason to believe, the so-called pterygoids of Crocodilus are really homologous with the amphibian parasphenoid, then either the amphibian pterygoid is unrepresented or we must look elsewhere for it.

The amphibian pterygoid is a well developed bone and in its various forms gives evidence of a high degree of adaptability so that we are not justified in assuming its disappearance from the reptilian skull. More especially does this contention gain weight when it is remembered that such an assumption would be to single this bone out, for all the other component bones of the amphibian skull are recognisable in the reptilian.

In a search for a true representative of the amphibian pterygoid in the reptilian skull, our attention naturally first falls on the os transversum or ectopterygoid.

The greatest objection to accepting this as the missing bone is probably its anterior situation, an objection founded, however, on difference in degree rather than of kind, and completely met by the citation of the situation of the pterygoid in *Ichthyophis glutinosus*.

In this the pterygoid is so similar in form and situation to the reptilian ectopterygoid as represented in the crocodilians that either the homology of reptilian ectopterygoid and amphibian pterygoid must be conceded or it must be contended that Ichthyophis is aberrant and possesses ectopterygoid and no pterygoid.

I anticipate that habit of thought will be one of the great obstacles to the acceptance of the thesis I am defending, and in the case of Crocodilus I found myself wasting much time and energy to convince myself that the old habit was wrong. The descriptions given above are founded on my original material, and the novel feature was clearly shown therein; yet force of habit caused me to doubt the evidence of three specimens only, and I wrote to Professor S. J. Johnston to search his collection for a median suture, and I advertised in North Queensland and purchased upwards of fifty skulls in vain search myself and have been unable to find the mythical suture. Dr Johnston failed to find it. Thanks to his kindness, I have had the opportunity of examining a Gavial skull 140 mm. in length and an alligator 95 mm. in length preserved in the museum of comparative anatomy of the Biology Department, Sydney University. Neither skull exhibits the mythical median suture of the parasphenoid.

THE CHELONIANS

The Chelonian skull, though aberrant in one or two respects, exhibits a degree of primitiveness which places them next on our list.

These skulls are aberrant in the absence of prevomers and osa transversa. They are primitive in the expanded form and in the situation of the pterygoids, and they are peculiar in the remarkable development of the vomer proper.

Chelonia midas (fig. 11) seems to exhibit just what happened to the conjoint pterygoid as developed in the crocodiles. The two pterygoids represent the body, naso-palatine and naso-mural elements, whilst the vomer, placed between the palatines, grooved above to receive the intorbital septum and produced into a spur on either side to articulate with the prefrontal, recalls the vomerine portion of the bone.

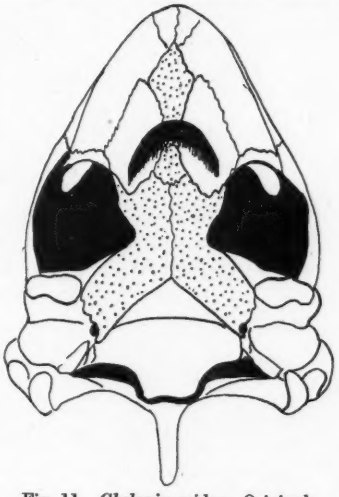


Fig. 11. *Chelonia midas*. Original.

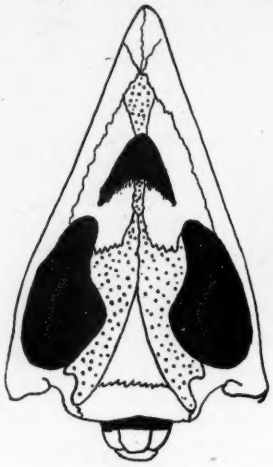


Fig. 12. *Chelonia imbricata.* Original.

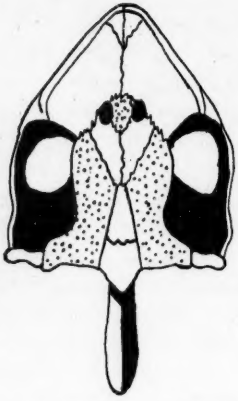


Fig. 13. Trionyx. From Zittel.

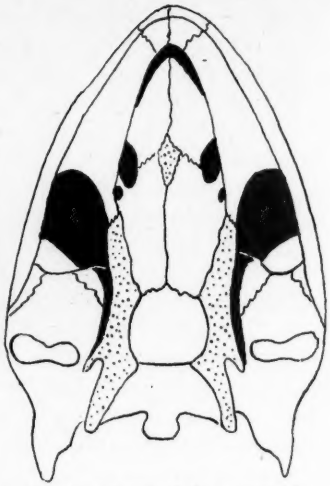


Fig. 14. Carettochelys. Original.

In the next three figures, 12, 13 and 14, we see three stages in the separation of the pterygoids from the midline.

Before leaving this group, it is of interest to note that here in the presence of a median vomer, as in the crocodilians in the presence of a vomerine plate to the conjoint pterygoid, it is not possible to demonstrate the existence of that median splinter developed below the intorbital septum and attached to the under surface of the fore end of the rostrum basisphenoidei, which has been designated parasphenoid, but which as it represents part only of that bone as developed in the amphibia is better designated vomer in accord with the teaching of Broom.

SOME PERMIAN FOSSILS

Before passing on to the recent Lizards, it were well to note the form of the pterygoids in a few Permian fossils.

Pareiasaurus (fig. 15) presents a much expanded pterygoid, recalling that of the crocodiles, prevomers are developed and the os transversum is present.

Nothosaurus (fig. 16) as figured by Zittel after Quenstedt is a striking skull in which the paired pterygoids extend forward to in front of the anteriorly situated choanae. This palate needs re-examination.

Ptychognathus (fig. 17) recall the chelonian in the absence of prevomers and ectopterygoids.

Scylacosaurus (fig. 18) exhibits an approach towards the form of pterygoid present in the Lacertilia but differs therefrom in their approximation to the midline and the resulting interpterygoid suture.

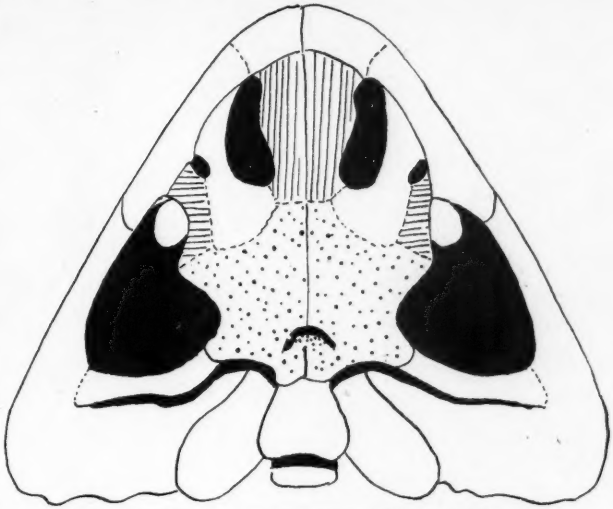


Fig. 15. Pareiasaurus. From Broom, *Bull. Amer. Mus.* 1910.

Procolophon (fig. 19), and Pariotichus (fig. 20) complete our series of fossil forms; the last presents all the features of Sphenodon (fig. 21) or Amphibolurus (fig. 22). Rhyncocephalia and Lacertilia are represented by Sphenodon (fig. 21), Amphibolurus (fig. 22) and Tiliqua (fig. 23).

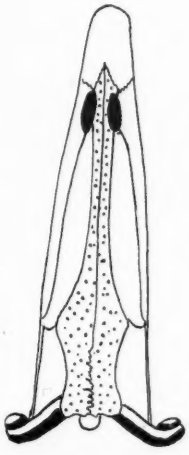


Fig. 16. Nothosaurus. From Zittel, *Palaeontology.*

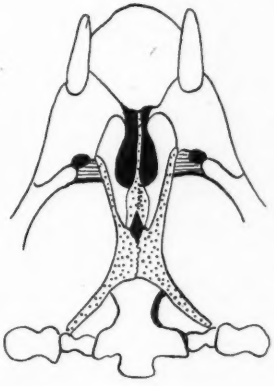


Fig. 17. Ptychognathus. From Broom, *Proc. Linn. Soc. N.S.W.* 1902.

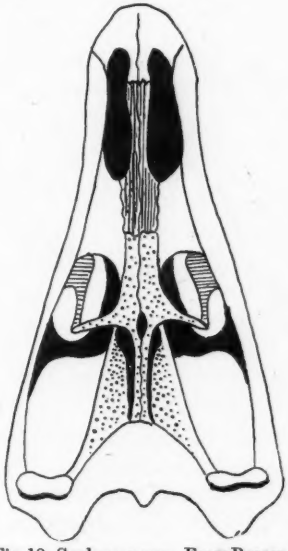


Fig. 18. Scylacosaurus. From Broom, *Bull. Amer. Mus.* 1910.

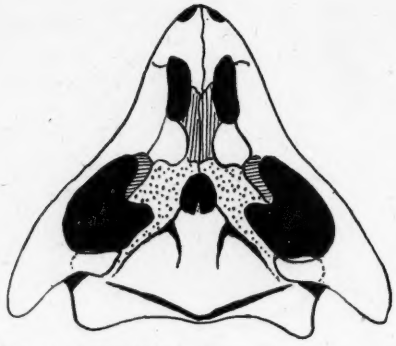


Fig. 19. Procolophon. From Broom, *Bull. Amer. Mus.* 1910.

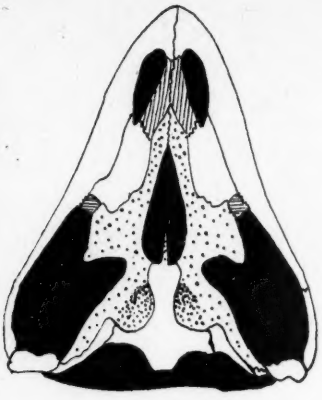


Fig. 20. Pariotichus. From Broom, *Bull. Amer Mus.* 1910.

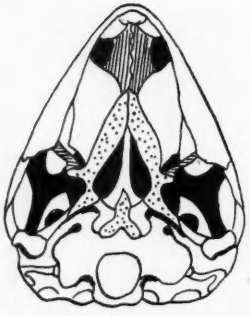


Fig. 21. Sphenodon. From Howes and Swinnerton.

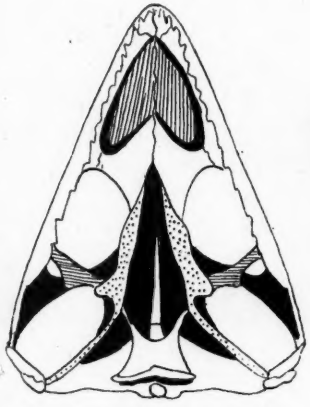


Fig. 22. Amphibolurus. Original.

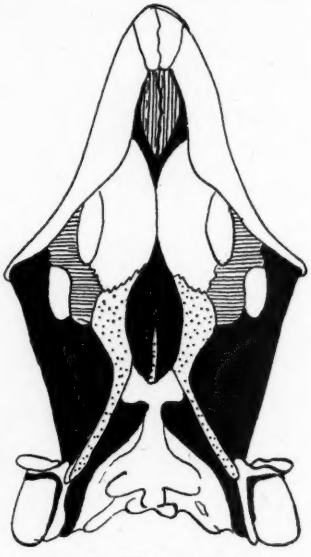


Fig. 23. Tiliqua. Original.

CONCLUDING DISCUSSION

"In the most primitive reptilian order with which we are acquainted —the Cotylosauria—we find that the palate differs from the ancestral Labyrinthodont condition mainly in the greatly increased development of the pterygoids, with a corresponding decrease in the size of the median vomer. Howes has already recently suggested that the reduction in the 'parasphenoid'

in the reptilian series has been brought about by the increased development of the pterygoids; and it seems moderately certain that this is the true explanation. It is more difficult to assign a cause for the increased development of the pterygoids."

This quotation from Broom's paper on "Mammalian and Reptilian Vomerine Bones" is of particular interest here. It emphasises the remarkable development of the pterygoids in the earliest of the known reptiles, suggests some correlation between the development of the pterygoids and of the parasphenoids, and in its last sentence expresses a difficulty which all thoughtful comparative anatomists must have felt when studying the bones on the palatal aspect of the amphibian and reptilian skulls.

A re-examination of my figures must convince one that at least within the reptiles the primitive situation of the pterygoids was along the base of the skull. These figures I publish are for the most part taken from other workers, and serve to point the fact that among the early fossils the predominant situation was as stated. It follows then that the modern form, as represented in the Lacertilia is evolved from an expanded pterygoid placed immediately below the neurocranium and meeting its fellow in a median interpterygoid suture.

Now if it be correct that the pterygoid of Rana and of Tiliqua are really the same bone, we must assume either that both are derived from an ancestral pterygoid approaching that of Loxomma in form and situation or we must assume that the reptilian has evolved from the amphibian pterygoid as presented in Rana or Branchiosaurus.

A third assumption would be an hypothetical ancestor possessed of a pterygoid presenting either the features of both or features intermediate between the two; such an explanation would, however, be entirely fanciful and is unnecessary. We are left with two alternatives, neither of which is satisfactory.

To assume a pterygoid ancestral to both approximating to that of Loxomma would be an assumption nearly as fanciful as the third, founded as it would be on the single instance of Loxomma itself, explaining only the two forms of pterygoid, and taking no notice of the lost parasphenoid and newly developed ossa transversa.

To assume, as has tacitly been done in the past, that the reptilian pterygoid is evolved from the amphibian as in Branchiosaurus leads us to the acceptance on faith of a complex of changes for which no explanation whatever is forthcoming. We must admit (1) that the first reptilian pterygoid developed was similar to that of Loxomma (i.e. it somehow developed forward along the midline losing its relation to the orbit postero-laterally), (2) later it loses its function as a basal covering bone and assumes the situation seen in Tiliqua, (3) meanwhile, also inexplicably, the parasphenoid disappears almost completely, persisting only in its forward part as the median vomer, and (4) two accessory bones, the ossa transversa, are developed.

Turning now to the explanation which is offered in this paper. The pterygoids of Rana and Tiliqua are not the same bone, but the os transversum of Tiliqua is the same bone as the pterygoid of Rana.

The parasphenoid is not correspondingly decreased as the pterygoids are developed, but persists as the pterygoids which in their primitive form occupy the situation of the single bone they replace.

An exceedingly significant fact which must not be overlooked is that there are no intermediate stages. Either we find a fully developed parasphenoid and pterygoids of the Rana type or we find no parasphenoid (except the vomer) and pterygoids of the Loxomma-Chelonia-Tiliqua type.

The conclusion arrived at would perhaps be best embodied in convenient language by henceforth designating the amphibian parasphenoid *conjoint* or *mesopterygoid*; the term parasphenoid should lapse, and the amphibian pterygoids should be termed *ossa transversa* or ectopterygoids.

GLADSTONE,
QUEENSLAND.
January, 1918.

NOTES ON MR KESTEVEN'S PAPER ON THE PTERYGOIDS IN AMPHIBIA AND REPTILES AND THE PARASPHENOID.

By D. M. S. WATSON, M.Sc.

Although Mr Kesteven's thesis that the amphibian pterygoid is homologous with the reptilian ectopterygoid and the reptilian pterygoids are separated parts of the amphibian parasphenoid is at once invalidated by the facts mentioned subsequently, his paper will serve the useful purpose of clearly indicating some of the problems presented by the varied structures of the palate in the two classes considered.

The following corrections on points of fact are necessary.

1. Embleton and Atthey's account of the palate of "Loxomma" is incorrect not only in many details but in general, owing to their belief that the choanae were far back as in a crocodile. The real posterior nares are the small openings lettered *Ap*. The median ridge labelled *R*, is part of the parasphenoid, which in this amphibian is a long laterally compressed bone sheathing the lower edge of the ossified orbital septum. The less clearly-marked fragments continuing this ridge backwards are parts of the same bone. The pterygoids are clearly separated throughout their length, and articulate by definite surfaces with the basipterygoid processes which lie to either side of the end of the reference line *B.s.p.h.*

The bone labelled *P.p.max.*, is divided in two by a suture, the anterior part being the palatine, the posterior the ectopterygoid. The bone labelled ectopterygoid is a broken part of the pterygoid.

I have already published a description of this palate founded on a large amount of magnificently preserved material.

The "Loxomma" type of palate is the only one known in Lower Carboniferous and Coal Measure Labyrinthodonts, it is shown in specimens of at least seven genera. It also occurs in the only known Coal Measure Leptospondyls. In a paper in the *Phil. Trans.*, 1919, I have described a series of Labyrinthodonts leading from this type of palate to a typical labyrinthodont type with a large parasphenoid and large interpterygoid varieties. The vast majority of these amphibia, including the latest and most typically amphibian, retain a typical ectopterygoid, so that it is quite impossible for this bone to be the homologue of the amphibian pterygoid. The Rana type of palate is so far from being the most primitive and commonest amongst amphibia, that it is restricted to the Batrachia Salientia and Branchiosauria, the ⊥ parasphenoid not occurring in a typical form in any other group. It has been shown by Meek and Shiino that in embryos of Crocodilus there is a small median parasphenoid in its usual reptilian position, and Leeds and

Andrews have shown that in the Jurassic crocodile Metriorhynchus there is in adults a large median parasphenoid forming the roof of the naso-palatine canals and completely separating the pterygoids above that passage. Finally in Crocodilus, as in all other reptiles, the pterygoids develope in association with the palato-quadrate cartilage.

Versluys has shown that a very large median parasphenoid is present in the adult skull of Dermochelys, and a small parasphenoid is present in the usual position in the developing skull of Emys.

Lastly it may be noted that the vomer of Chelonia is shown by its development to be a fused pair of prevomers.

There is in fact no doubt that the Loxomma palate, which greatly resembles that of Osteolepid fish, is the primitive Tetrapod type, that with only slight modification it leads directly into the reptilian palate and by increase of size of the interpterygoid varieties and of the parasphenoid it passes into that characteristic of the amphibia, the whole process being shown in the Order Labyrinthodontia.

March 8th, 1919.

THE CAPACITY OF, AND THE PRESSURE OF FLUID IN, THE URINARY BLADDER

By RALPH THOMPSON, Ch.M., F.R.C.S.,

Surgeon in charge of the Genito-Urinary Department, Guy's Hospital.

The object of this paper is to draw attention to the following points in connection with the urinary bladder.

First; the small capacity of the urinary bladder in the living state, when compared with the capacity indicated by various authors, presumably from experiments made in the dissecting room.

Secondly; the bladder, being a muscular organ, should be used as such.

Thirdly; the bladder, being a muscular organ, is capable of exercising pressure upon its contents.

Fourthly; the bladder, like other abused muscular organs, is capable of failure, the liability to which is enhanced, and the cure of which is retarded, by the teaching of certain text books on the subject.

PART I

CAPACITY OF THE BLADDER

By the term "capacity" should be meant that amount of fluid, which, under normal circumstances, gives rise to the desire to micturate, and it is according to this definition that the term "capacity" will be used. Some of the authors of recognised text books on anatomy do not attempt to define the term, but it may be confidently assumed that they mean that amount of fluid which can be contained in the bladder found in the dissecting room. Thus the following statements are made by recognised authorities, whose works are consulted commonly.

Professor A. Macalister states, in his work on Human Anatomy, that "the average capacity of the Urinary Bladder is 650 c.c. and lies between the limits of 450 and 1600 c.c. in the male, and 320 and 1300 c.c. in the female." Professor Johnson Symington in the 10th edition of Quain's *Anatomy* states that "the urinary bladder has an average capacity of about 1 pint (11th edition 500 c.c.) when moderately filled, but is capable of being distended to a considerably greater degree."

Professor R. Howden in Gray's *Anatomy*, 1913, states that "when the bladder is moderately full it contains about 0·5 litre."

Professors John Cleland and Yule Mackay, and Professor J. Playfair McMurrich do not commit themselves by stating any capacity.

Professor Francis Dixon in Cunningham's *Text Book*, 2nd edition, p. 1150, states that "the bladder in normal distension may contain as much as one

pint, but, in most cases, the organ is emptied when its contents reach from six to ten ounces," a statement with which the writer is in cordial agreement, as it shows that the author is alive to the importance of the study of living anatomy.

Professor J. Albarran in his book *Médecine opératoire des voies urinaires*, distinctly indicates that he, also, is bearing in mind the living bladder when he says that " lorsque la vessie normale contient 250 ou 300 centimètres cubes d'urine, le besoin d'uriner se fait sentir."

Mr Thomson Walker in his *Genito Urinary Surgery*, p. 344, states that "the physiological capacity of the bladder is from 8 to 10 ounces, but it may be so distended, as to contain several pints, or even quarts."

Zuckerkandl and Franck Hochwart, as quoted by the last named authority, state that "in normal individuals there is slight desire to micturate when 100 to 500 grammes are introduced into the bladder, and the pressure varies from 10–30 cm. of water." This is a statement which is so very vague that it certainly demands amplification and explanation.

Now whatever be the actual capacity of the bladder I am certain that students have very wrong ideas about its amount. This may be due to lack of conception of any quantity, be it large or small; but I have very frequently most exaggerated accounts given of the capacity of the bladder, which have to be modified very considerably. Bearing in mind that about 1500 c.c. of urine are secreted in 24 hours and that during that period this quantity is passed from the bladder by about five micturitions we see that the capacity of the bladder is about 300 c.c., if the definition given previously be accepted. Five times may be considered to be a minimum number in 24 hours, and, therefore, 300 c.c. may be considered to be a maximum during the waking hours (the amount which is passed in the morning after rising from bed will be considered later). In a series of observations, 138 in number, made by me upon seven patients, adult and healthy, the following records were made irrespective of the desire of the patient to micturate.

The smallest quantity passed was 55 c.c., the largest quantity 560 c.c. This latter quantity was collected between the hours of 8 a.m. and 6 p.m. Not in one case was the quantity of one pint reached. The mean of the mean quantities which were passed by the seven patients was 211·5 c.c. The times during which the various quantities were collected since the last micturition, according to the patients' own accounts, were recorded, and the average period of collection of 211·5 c.c. of urine was 2·687 hours, which is equivalent to a mean rate of flow from the kidneys of 78·47 c.c. per hour. These figures are given as they show that the renal outflow need not be taken into account in the following experiments conducted by me in order that the capacity of the bladder might be, if possible, determined more accurately.

These methods of estimating the capacity of the bladder are open to some objection, and so it became necessary to devise some more accurate method.

This I was enabled to do, by noting in one case under my care for chronic gleet, that the patient passed fluid by the side of a small catheter from his bladder—the fluid being used for irrigation purposes.

Acting upon the information obtained in this case I have devised the following method for estimating the capacity of the bladder.

The fluid used for irrigation purposes is 1 in 10,000 potassium permanganate solution—of a temperature at the beginning of 120° F.; but by the time the fluid enters the bladder it is probably considerably less. This solution is no more irritating when applied to the eye than is normal urine.

A funnel of capacity 1600 c.c., is suspended at a height of $1\frac{1}{2}$ metres above the patient, who is laid in a recumbent position upon a couch. A catheter, with two conical protuberances at its bladder end, whose bases face each other and are perforated, and of size approximately No. 4 English size is introduced into the bladder. Any urine in the bladder is removed. The catheter and funnel are connected to the tube of the funnel by Wyndham Powell's irrigator. Taps are provided in the tube of the funnel, as it was found that during micturition fluid entered the bladder at a greater rate than it was discharged, thus possibly leading to vitiation of the results. By means of the taps fluid from the funnel could be prevented from entering the bladder during micturition. The fluid was allowed to fall into the bladder by the action of gravity, and the patient was instructed to micturate when he so desired. This he did through the urethra *by the side of the catheter*. The following simple method was adopted for collecting the fluid passed at each micturition. A curved lead tray, appropriately shaped, and whose edges were turned over so as to diminish leakage by splashing was introduced between the thighs—a notch was cut in its upper edge for the reception of the penis. Thus the upper part of the tray lay upon the patient's pubes and scrotum, and upon the upper and front part of the thighs.

The lower edge of the tray was narrower than the upper part, and rested upon a pot sink, made by Messrs Doulton, let into the couch. This sink sloped downwards and terminated in a hole leading to a tin pipe which conducted the fluid away. This tin pipe opened at its other end into a succession of glasses which were arranged upon a small stool, the top of which could be rotated a little, when one glass had received the fluid passed during a single micturition, so that a separate glass could receive the fluid passed during the next micturition. By this means, the fluid passed at successive micturitions could be collected and measured. I found that the apparatus had an error of 20 c.c., a quantity which is practically negligible.

The quantities passed were measured, recorded and charted.

Eight patients were observed. The mean quantity passed by each patient (all males) was as follows: (1) 326, (2) 275, (3) 244, (4) 229, (5) 215, (6) 181, (7) 150, (8) 126 c.c. With the exception of the first patient who was not so big as some of the other cases observed, but who was muscular and well developed, the quantity of fluid, which was passed, corresponded to the size

of the patient—being more with the bigger patients; so that the conclusion may be drawn that the capacity of the bladder increases with the size of the individual, rather an important practical point, when it is required to introduce fluid into the bladder for the purpose of such proceedings as lithotrity, or cystoscopy, or irrigation of the bladder. As an unequal number of observations were made upon each patient the mean of the mean quantities is taken, and found to be 218 c.c., which may be regarded therefore as that amount of fluid which gave rise in these patients to the desire to micturate. The highest mean quantity passed was 326 c.c.—the lowest 126 c.c. The highest quantity passed was 400 c.c.

From these observations we may conclude that *the mean capacity of the bladder of the living male adult is* 220 *c.c. but varies between* 120 *c.c. and* 320 *c.c.*

Some of the charts of the records that were made of the quantities, which were passed during successive micturitions, are worthy of attention. The quantities varied; but in many cases they varied regularly—so regularly in some cases that the mean quantities which were passed at successive micturitions were also found to present regular variations. The variations observed in the quantity of fluid passed by the bladder can be summed up thus:

(1) A single minimum quantity was succeeded by a single and larger quantity and after this regular alternation of minimum and maximum quantities were observed—sometimes the quantity varied to the extent of as much as 100 c.c. (fig. 1).

[This and the three following figures represent *quantities* only which are passed at each micturition.]

(2) Two maximum quantities might be passed in succession followed by a decrease in the quantity which was again succeeded by a double maximum (fig. 2).

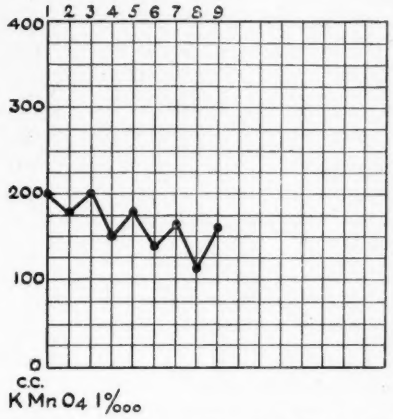
(3) A small quantity might be passed at the beginning of the observation followed by increased alternative maximum and minimum quantities (fig. 3).

(4) A large quantity might be passed at the beginning of the observation followed by decreased alternations of quantity (fig. 4).

Whatever the explanation may be of these regular variations they may be considered to indicate a vital muscular activity of the bladder which must not be disregarded by anatomists in their estimate of the capacity of the bladder, which in many cases, as has been shown, is regarded as a dilatable inert bag.

The succeeding part of this paper will be devoted to the consideration of pressure in the bladder. Although this question is one of physiological importance it appears to me to be of interest to anatomists, and as by an investigation of the pressure in the bladder evidence may be brought forward which confirms that which has been insisted upon already, namely that the bladder is a contractile muscular organ, and demonstrations of its possible

degree of distension in the dead body are of no value to the anatomist. With an active and energetic student, and a strong syringe, at one end of a catheter, and the bladder of a dead man at the other end, I am surprised that anato-



Figs. 1—4 represent *quantity only* of fluid passed at each act of micturition. This figure shews alternating maximum and minimum quantity[1].

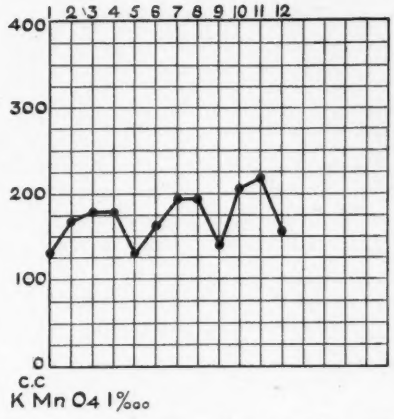


Fig. 2. To shew two (or three) maxima alternating with one minimum.

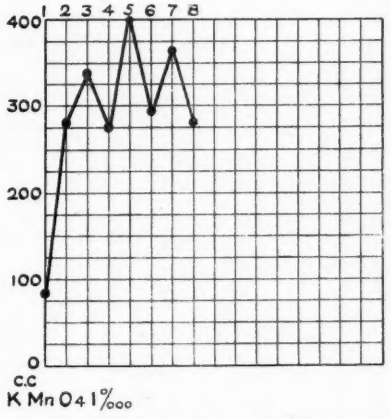


Fig. 3. To shew small quantity passed at first micturition followed by alternating maxima and minima of larger quantity.

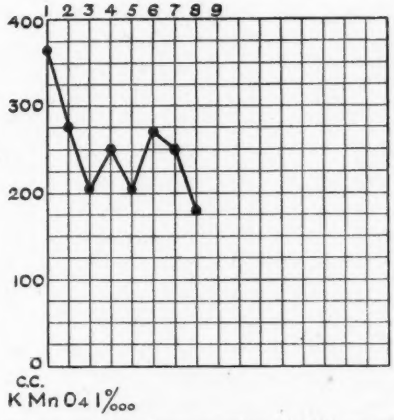


Fig. 4. To shew large quantity of fluid passed at first micturition followed by alternating maxima and minima of smaller quantity.

mists have stopped short at the quantities they have stated; but we are concerned with a living man's active muscular bladder.

[1] In Figs. 1—4 and in Fig. 13 the horizontal line of numbers at the top of the chart represents successive actions of the bladder.

PART II

PRESSURE OF FLUID IN THE BLADDER

My observations of the pressure of fluid in the bladder may be thrown conveniently into a connected account as the results unfolded themselves to me.

Evidence of failure of the bladder muscle to discharge fluid from the cavity is common in the outpatient room of a hospital. This evidence will be adduced later. It will be sufficient now if we recognise its existence. First, then, we may consider the pressure of fluid in a bladder which has failed completely—and then consider observations on bladders which are only feebly active, and, finally, observations on bladders which have not failed but are still active muscular organs.

I. PRESSURE OF URINE IN BLADDERS WHICH HAVE FAILED.

A typical observation, the results of which are charted in fig. 5, is as follows:

The patient observed was aged 72 with an enlarged prostate and absolute retention, i.e. a catheter had to be passed every time there was the desire to micturate. Otherwise the patient was very healthy, of a good colour, and sound circulation.

[The method of investigation adopted in this and succeeding observations was as follows. The patient was laid in the recumbent position upon a couch—a catheter was introduced into the patient's bladder and connected by a tube with a three-way tap conducting to a mercury and a water manometer. The three-way tap was introduced in order to avoid the complication of urine getting into the manometers—as a matter of fact it was not used as, if wanted, it could not be brought into action quickly enough. The level of the manometer was noted at various times, and immediate records made.]

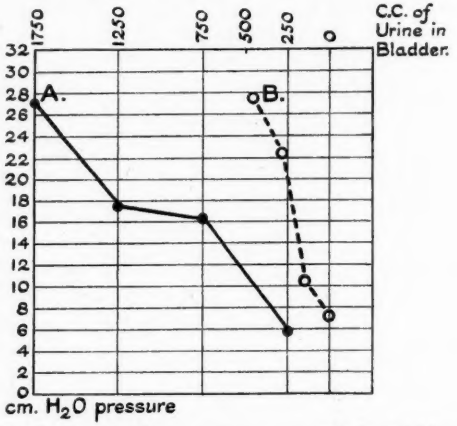


Fig. 5. To shew decrease of pressure with diminishing quantities of fluid in bladder,
A which has failed;
B which is still active.

The above clinical observations having been made it was found that the bladder formed a large tense palpable mass in the lower half of the abdomen, which extended up to the umbilicus, and spread widely on each side of the middle line.

With a quantity of urine amounting to 1750 c.c. the pressure recorded was 27·5 cm. H_2O; with 1250 c.c. pressure sank to 17·5 cm. H_2O; with 750 c.c. pressure only sank slightly to 16·5 cm. H_2O; but with 250 c.c. only in the bladder the pressure sank to 5·5 cm. H_2O.

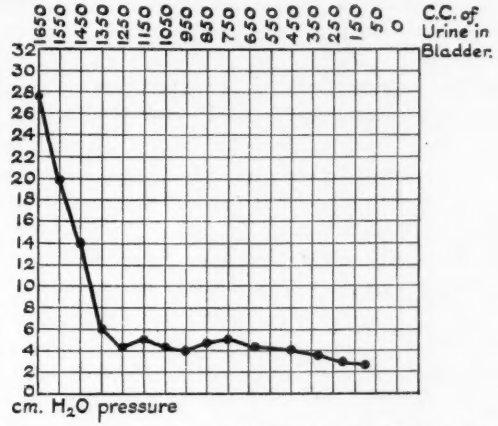


Fig. 6. To shew descent of pressure in a bladder which has failed and from which regular quantities (100 c.c.) of fluid have been removed.

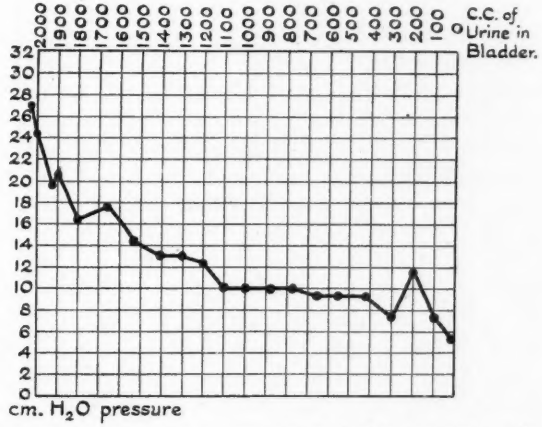


Fig. 7. To shew descent of pressure with diminishing quantities of fluid.

If the records are plotted as a curve (fig. 5) there is manifested a rapid descent followed by a slow descent, succeeded later by a rapid descent. The first rapid descent which takes place even when quite small quantities of fluid are removed is, doubtless, to be associated with the sudden diminution in the tenseness of a dilated bladder as indicated by abdominal palpation—a diminution which may lead to possible failure in recognising a bladder which

may, however, contain a large quantity of fluid. There is also another form of chart from another individual in which after the rapid descent produced by the removal of a small quantity of fluid the pressure remains pretty much the same, but with a general diminution when successive and equal quantities of fluid are removed from the bladder (fig. 6). The preceding chart (fig. 7) shows a more gradual but progressive decrease in pressure with diminishing quantities of fluid in the bladder. In these two charts records of increased pressure with decreased quantity of fluid in the bladder are apparent—it may be that a maximum pressure was recorded in one observation and a minimum pressure in another; if so, then these bladders have not absolutely failed but are showing conditions which become more apparent in other and succeeding cases—namely, waves of pressure set up by a muscular bladder.

II. Pressure of urine in bladders which have only failed partially.

The case illustrating this condition is as follows. The man was aged 58 with bad arteries, and a heart which gave out one day leading to sudden death —a partial post mortem examination was made. There was no stricture, and the prostate was not enlarged, and we may, therefore, conclude that the bladder had taken part in the general failure of the individual.

The patient had difficulty in passing water, but no obvious obstruction was noted clinically. During one observation, in life, the following conditions were noted.

The bladder was palpable, projected to the right, and reached nearly to the level of the umbilicus. The bladder held, at least, 450 c.c. During successive observations of the pressure it was found that there was a maximum and minimum pressure. This clearly shows a distinct advance upon previous observations from which variations of pressure could be only assumed. Thus:

A. with 450 c.c. in bladder

maximum pressure was	43·6 cm.	H_2O
minimum „ „	39·6	„
difference	4·0	„

B. with 350 c.c. in bladder

maximum pressure was	31·6 cm.	H_2O
minimum „ „	28·2	„
difference	3·4	„

C. with 250 c.c. in bladder

maximum pressure was	16·2 cm.	H_2O
minimum „ „	13·6	„
difference	2·6	„

D. with 100 c.c. in bladder

maximum pressure was	11·2 cm.	H_2O
minimum „ „	9·2	„
difference	2·0	„

Thus, in this case, not only are there diminishing pressures with diminishing

quantities of fluid, but the differences between maximum and minimum pressures also diminish.

It may be concluded, from these observations, that waves of pressure are set up in such a bladder the mean height and the amplitude of which vary with the quantity of fluid in the bladder.

The next case may possibly add to the information already given.

III. Pressure of urine in bladders which are active.

The patient, forming the subject of the succeeding observations, was a feeble looking man with bad kidneys, who attended my outpatient department owing to retention of urine, and difficulty in passing it.

On palpation of the abdomen, it was found that the bladder formed a hard, elongated sausage-like mass, which projected upwards to the level of the umbilicus, and lay more on the right side than on the left side of the middle line. I was at once struck by its shape and extraordinary hardness and absence of fluid tension. The patient had a stricture situated in the usual position in the urethra:—it felt "gritty" and was tortuous. A No. 4 catheter was passed and connected up with the water manometer. The mean pressure of water was 27·2 cm. but there were, clearly, waves of increased, and decreased, pressure. These waves presented a rapid ascent, and a slow descent. The descent appeared to occupy about five or six times the time occupied by the ascent. 170 c.c. were drawn off from the bladder and the pressure sank to 22·7 cm.—a further 150 c.c. was drawn off and the pressure fell to 10·5 cm., —a further withdrawal of 120 c.c. was associated with a fall of pressure to 7·5 cm. H_2O. Thus in this man's bladder, which was an active one, the pressure sank more regularly and more constantly than in corresponding observations upon bladders which had failed (fig. 5).

Three days after this observation was made the patient was examined again. An attempt was made to observe and record the manometer readings every 15 seconds at first, and later every 10 seconds. The records were then charted (fig. 8).

The rapid ascent and slow descent are displayed clearly but especially so in the last three waves.

The first observations were made with 500 c.c. in the bladder; the last observations were made with 250 c.c. in the bladder. This chart confirms the truth of previous observations, namely, that waves of pressure are set up in an active bladder, i.e. a bladder with an active muscular wall; and that the mean height and amplitude of the waves vary as the quantity of fluid in the bladder. There can be no doubt that these waves were produced by muscular action. The patient was a quiet and phlegmatic man, and his respirations and pulse were normal.

The next observation on this patient was made with a tambour and double lever manometer, and showed a wave of pressure precisely similar to those recorded. The descent of pressure occupied about 2 minutes. The

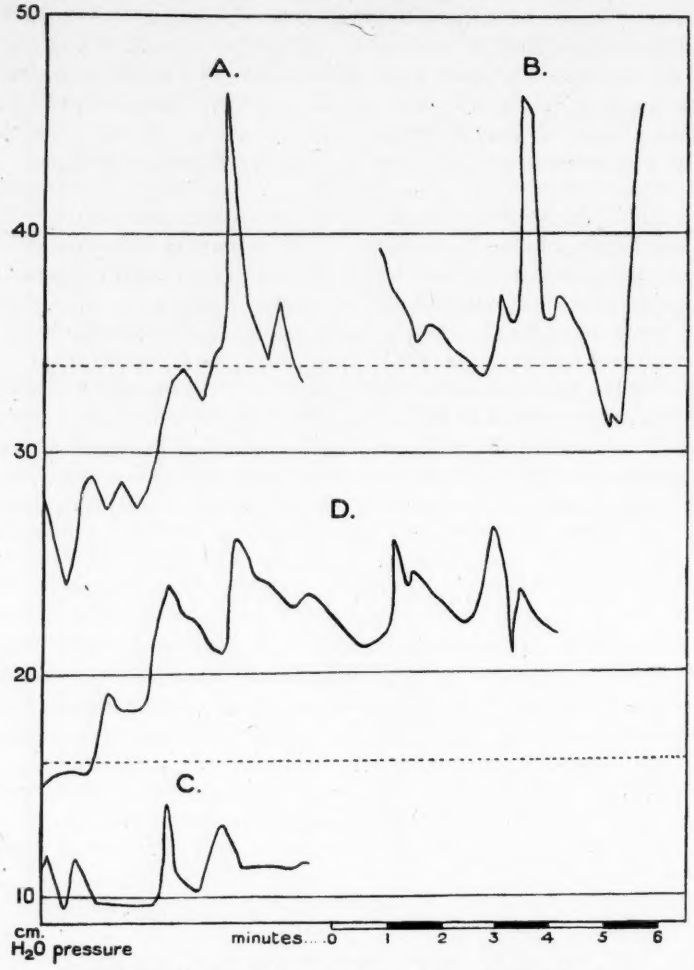


Fig. 8. Shewing waves of pressure set up in a contracting bladder.

The chart is constructed upon observations made with a water manometer;

In A and B observations were made every 15 seconds, and the bladder was holding 500 c.c. of urine.

Maximum pressure was 46·2 cm. H_2O; Minimum pressure was 23·6 cm. H_2O;
Mean pressure was 34·28 cm. H_2O;

(Additional observations taken into account but not recorded here.)

There is an interval of 5 minutes between A and B.

In C observations were made every 10 seconds, and the bladder was holding 250 c.c. of urine.

Maximum pressure was 14·2 cm. H_2O; Minimum pressure was 9·4 cm. H_2O;
Mean pressure was 10·77 cm. H_2O.

There is an interval of 10 minutes between B and C.

In D observations were made every 10 seconds, and the bladder was holding 250 c.c. of urine.

Maximum pressure was 26·8 cm. H_2O; Minimum pressure was 14·8 cm. H_2O;
Mean pressure was 21·27 cm. H_2O.

There is an interval of 5 minutes between C and D.

The dotted lines indicate, in the case of the upper one, the mean pressure with 500 c.c. of urine in the bladder; and in the case of the lower one, the mean pressure with 250 c.c. of urine in the bladder.

Fig. 9. Active contracting bladder holding 500 c.c. of weak Collargol. Magnification $\frac{5}{4}$ at base, $\frac{1}{1}$ at apex.

Fig. 10. Active contracting bladder holding 400 c.c. of weak Collargol. Magnification as in Fig. 9.

Fig. 11. Active contracting bladder holding 250 c.c. of weak Collargol. Magnification as in Fig. 9.

Fig. 12. Bladder holding 150–200 c.c. of weak Collargol. Magnification as in Fig. 9.

ascent about 15 seconds. In the ascent there was, about the middle of its course, a double flexure producing the impression of a step in the ascent. The descent formed a regular slope.

From this case it may be concluded that in an active bladder waves of pressure are set up due to muscular action. These waves show decreased mean height, and decreased amplitude, as the quantity of fluid in the bladder is diminished. The mean pressure with 500 c.c. in bladder was 34·28 cm. H_2O; with 250 c.c., 16·02 cm. H_2O.

Skiagrams have been taken of this man's bladder containing known quantities of weak collargol. Tracings of these skiagrams were made and are reproduced in figs. 9, 10, 11 and 12. They show an appearance suggestive of a contracting organ, as the general shape is maintained in all the figures which could hardly be expected to be the case if the bladder had failed and become a mere inert bag, in which case the upper portion in the figures would be more rounded, i.e. convex laterally and more prominent, than is indicated in the skiagrams. From these observations we may conclude that the mean capacity of the urinary bladder is about 220 c.c. varying between 120 c.c. and 320 c.c. with the size of the subject; also, that definite pressure is exercised by the bladder upon its contents—varying with the quantity of fluid it contains; and that the bladder, like other muscular organs, may fail if improperly used, or abused.

This last statement requires some evidence which requires to be stated afresh. Civiale long ago drew attention to its occurrence. The proofs in this paper depend upon experimental and clinical evidence.

Failure of bladder

I. Experimental evidence.

In the irrigation experiments which were recorded in the first part of this paper, some cases occurred (which were not taken into account in arriving at a mean capacity of the bladder) in which after a series of regular alternating quantities passed from the bladder, the quantity steadily diminished, the bladder became palpable through the abdominal wall, and the patient eventually passed a fair quantity when he stood up and called the abdominal muscles into action. Such a case is graphically illustrated in the accompanying figure (fig. 13).

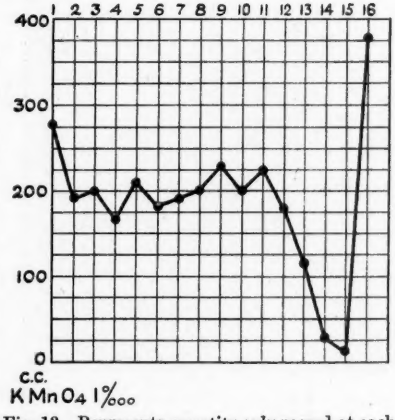


Fig. 13. Represents *quantity only* passed at each act of micturition.
Quantity charted under No. 16 was passed by individual in standing position.

The last observation showed that

385 c.c. were passed in the erect position, but that previous to this, and after a regular series of alternating quantities, the quantity passed at each micturition steadily and progressively diminished.

It must be remembered that in these observations the bladder is being used in half an hour as often as it is in three days usually, and the manifestations of its fatigue or failure, may be apparent in these experiments.

II. Clinical evidence.

A. In support of this the following case may be cited. The patient was a healthy adult with a bladder having a mean capacity of 150 c.c. One day he allowed nearly a pint to collect. He was only able to pass about 200 c.c., but when more fluid was introduced into the bladder by means of a funnel and tube it was stimulated to act, and patient passed a quantity of fluid from his bladder greatly in excess of his usual quantity.

B. Not infrequently patients are seen suffering from the later manifestations of chronic interstitial nephritis—in whom the urine consists practically of pure water, and which is therefore of very light specific gravity. No evidence of obstruction to the flow of urine is found during life or post mortem, but the bladder is distended with 1500 or 2000 c.c. of urine. These cases may be believed to be cases of primary failure of the bladder, associated with the general "break up" and the unirritating nature of the urine.

SUMMARY

1. The mean capacity of the living urinary bladder in the male adult is 220 c.c. varying from 120 to 320 c.c.

2. If fluid be introduced into the bladder and the subject be asked to micturate when he desires to do so, alternating but regular quantities of fluid are discharged.

3. The pressure of fluid in failing bladders diminishes with decreasing quantities of fluid but not constantly.

4. The pressure of fluid in active bladders diminishes with decreasing quantities but constantly. This pressure has a wave-like form, and the amplitude of the waves also diminishes.

5. Neglect of the muscular nature of the wall of the bladder has led several authorities to overstate the amount of its capacity.

6. The capacity of the bladder should not be stated as being above 320 c.c., as such statements may lead to inadequate conception of the rôle of the bladder amongst surgeons and medical men, with consequent production of failure of its muscle. This not only leads to retention of urine but also, most surely, to serious and grave disturbance of the lymphatic and venous circulation of the bladder and its surrounding parts.

The writer has, in possession, other records, e.g. of pressure in the bladder which is being filled gradually, as well as the amount of urine passed first thing in the morning by normal individuals. These may form the subject of a future communication.

ABNORMAL RIBS AND VERTEBRAE IN A HUMAN FOETUS

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Gonville and Caius College, Cambridge

(Communicated by W. L. H. Duckworth)

A human foetus dissected in the Cambridge Anatomy School during the Long Vacation, 1918, presented an unusual deformation of the ribs and vertebral column as described in the following paragraphs.

Fig. 1. Human foetus (Mus. Anat. Cant. specimen VH) with abnormal vertebrae and ribs. From vertex to coccyx the length was 202 mm.

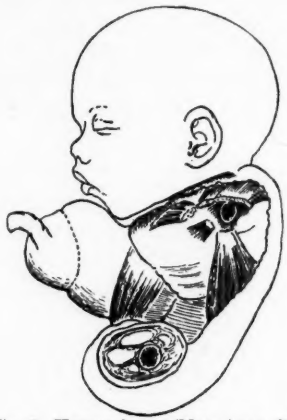
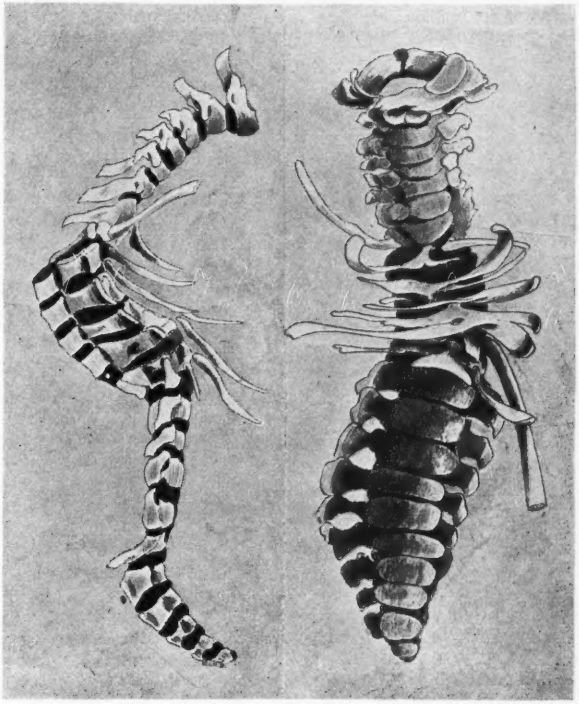


Fig. 2. Human foetus (Mus. Anat. Cant. specimen VH) with abnormal vertebrae and ribs. The limbs of the left side have been removed to exhibit the ventral hernia.

The specimen (Fig. 1) was a female measuring 200 mm. in length from the vertex to the coccyx. It seemed to have been born at some time during the seventh month of intra-uterine life, but no data were available as to its history. The most striking superficial features were a large ventral hernia (Fig. 2), and a large depressed scar-like area in the mid-dorsal line of the thorax and abdomen. The latter feature was clearly indicative of spina bifida, though no tumour existed. Dissection was commenced with a view to ascertaining the nature of the herniated mass, but in the course of the work the skeletal abnormalities associated with the hernia and spina bifida proved

to be exaggerated in degree and very rare in kind. Consequently the ribs and the vertebrae will be described first.

Ribs and Vertebrae (Fig. 3, *A* and *B*). The thoracic skeleton looked as though strong lateral compression had been exerted on its surface and on the right side the ribs were actually pressed inwards. Moreover the ribs were abnormal in number, only nine being identified on each side. In the vertebral column the neural arches were complete as far as the fifth cervical



B A

Fig. 3. Human foetus (Mus. Anat. Cant. specimen VH), with abnormal vertebrae and ribs. A, frontal view; B, side view of the vertebral column and ribs.

vertebra (inclusive) but beyond this tailwards the vertebral canal was open. Angular curvature of the column is pronounced at the disc between the first and second thoracic vertebral and a violent dislocation seems to have occurred here. For the first thoracic centrum (carrying the cervical vertebrae and the skull with it) appears to have slipped forwards (i.e. ventrally) abandoning the centrum of the second thoracic vertebra (Fig. 3, *B*). The first thoracic centrum has formed a new lower articulation as described in the sequel.

The two halves of the second thoracic neural arch have not merely failed to unite, but so far from moving dorsally as is usual, their pedicles have actually moved in the ventral direction (Fig. 4). So far have they swung thus, that they bound a ventral neural cleft. This narrow cleft is closed ventrally by a mass of bone representing the heads and necks of the two ribs (right and left) which at this level have coalesced in the median plane. The portion common to the two ribs is prolonged towards the cleft between the two pedicles of the neural arch. But a more surprising observation is that the same portion (common to the two ribs) actually supports the first thoracic vertebra, and consequently the vertebrae above this (cf. Figs. 3, *B* and 4).

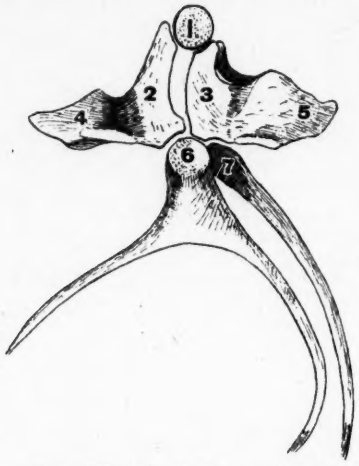


Fig. 4. (× 2 approx.) Human foetus (Mus. Anat. Cant. specimen VH) with abnormal vertebrae and ribs. Upper surface of second thoracic vertebra with associated ribs.

1. Centrum of second thoracic vertebra.
2, 3. Pedicles ,, ,, ,,
4, 5. Laminae with narrow elliptical intervertebral articular areas on their ventral margins.
6. Area of articulation with lower aspect of first thoracic centrum. This area is situated on the conjoined heads of the third right and left ribs.
7. Fourth rib of left side.

The laminae of the second thoracic vertebra project laterally and that on the left side (but not its pedicle) has coalesced with the following lamina (third thoracic vertebra).

The extraordinary conformation of the second thoracic vertebra is repeated in essentials by those that follow it as far as to the sixth. Thereafter the normal relation of centrum to centrum is re-established.

In addition to this dislocation, lateral curvature was detected, and the crowding together of the ribs may be assigned in part to the latter factor. Indeed a partial fusion of the ribs of the same side was observed in several instances. The last rib on each side ran towards the iliac crest to which a

strong fibrous band tethered it. Intercostal branches of the thoracic aorta seem to have been suppressed, and the sympathetic cord in the thorax descended as in Reptiles, i.e. in a position dorsal to the necks of the ribs.

One instance of coalescence of two successive neural processes has been mentioned above. In addition to this, the imperfect separation (or partial coalescence) of the fifth and sixth neural processes on the right side reproduces the same phenomenon, which recurs again on the left side, the seventh and eighth thoracic segments being involved here. The various distortions may be described as "pressure-effects" of some cause unknown. That the amnion is responsible cannot be alleged with confidence, though the probability is great. The process of events in the upper thoracic neural "arches" presents a certain analogy with that whereby the somato-pleural walls of the amnio-medullary cavity are displaced ventrally in consequence of the progressive increase in the contents of that cavity. Such speculation does not imply rejection of what may be termed "chemical" causes, such as those on which the late Professor Mall laid so much stress (Keibel and Mall; *Manual of Human Embryology*, Vol. I, p. 231).

The peculiarities of the ribs and vertebrae here described could doubtless be matched in other examples of Spina bifida. Specimens described by Dr J. P. Good (*Studies in Anatomy from the Anatomical Department of the University of Birmingham*, 1910) evidently owned similar deformities, but the latter are not figured in the publication mentioned.

The hernia. The hernial sac contained a large part of the liver together with most of the small intestine, the caecum with its appendix, and part of the colon. The caecum occupied a part of the sac corresponding to the proximal portion of the umbilical cord. The latter was much distended here. But though the caecum had not receded into the abdominal cavity, torsion of the alimentary canal had occurred, for the caecum is on the right side of the sac.

Abdominal contents. Apart from the general distortion of its form, the liver presented no anomaly of lobation. The ascending colon (traced backwards from the sac to the abdominal cavity) seemed to plunge into the mesentery above the small intestine, and then turned leftwards in the abdominal cavity towards the spleen. A further flexure brought the colon across to the right iliac fossa which was filled by a loop evidently representative of a pelvic colic loop. At first the condition seemed analogous to the abnormality of torsion described by Mrs Flemming in the *Proceedings of the Anatomical Society*, March 1897, but careful re-investigation showed that this is not the case. Apart from the peculiar relation mentioned above (whereby the "ascending" and "transverse" parts of the colon appeared to share the mesentery with the small intestine) the usual torsion of the alimentary canal was simply incomplete.

The peritoneum formed a distinct genito-mesentric fold (Reid) extending to the right iliac fossa where the fimbriated portion of the oviduct was bound down to the peritoneal floor of the fossa by a distinct fold with a curved margin. Beneath the duodenum a large "inferior duodenal" fossa was seen. In regard to other organs, the partial contact of the two kidneys was noticed, the left kidney having passed to the right, insinuating its upper pole behind the aorta. The adrenal bodies were likewise in contact but had not coalesced.

Thoracic contents. The absence of aortic intercostal arteries and the anomalous course of the sympathetic cord have been mentioned already. Here it may be added that a transverse communication between the right and left sympathetic cords was found on the centrum of the 7th cervical vertebra, the commissure in question being thickened and apparently ganglionic. The heart had a bifid apex and the right and left ventricular walls were approximately equal in thickness. The right lung had but two lobes and the costal aspects of both lungs were deeply channelled

by grooves corresponding to the depressed ribs. The latter were found to run towards a sternum in which no anomaly was detected.

Central nervous system. The spinal cord ended as a distinct "cord" at the level of the 5th cervical vertebra. Thereafter the cord was replaced by a "cauda equina," probably different in nature from the normal sheaf of nerve roots so designated. No anomalies of the limb plexuses were detected, although the exposure of the central nervous system below the 5th vertebra had been accompanied by much disintegration of the cord itself. No anomalous conditions appeared in the brain, but the falx cerebri was largely defective in its hinder portion, and the two hemispheres were in contact with each other in that region. Yet a superior longitudinal sinus was present, and the right superior petrosal sinus was represented by two offshoots from the cavernous sinus which were widely separated in the floor of the middle cranial fossa before they united to form a single vessel entering the transverse sinus.

In terminating this description, I have to thank Dr Duckworth for his aid in arranging the notes and in preparing the illustrations.

SOME OBSERVATIONS ON THE GASTRO-INTESTINAL TRACT OF THE HINDUS

By Dr N. PAN,

Professor of Anatomy, Medical College, Calcutta, India

The nature of the diet in Indians differs considerably from that of Europeans. In an Indian diet we find a bulky carbohydrate food with a very small proportion of the other proximate principles. This led me to expect that the anatomy of the gastro-intestinal tract in Indians would differ from that of Europeans to a considerable degree. Hence I took up this subject first and got some results which I intend to discuss in this paper. The observations were made on 65 subjects, a very small number, and the conclusions drawn from these cases must be accepted with caution. But this preliminary report, I presume, will not be far from the normal standard here and I have a mind to continue my observations in this line among others during the coming session.

SUBJECTS AVAILABLE FOR OBSERVATION

The subjects available for dissection in the Calcutta Medical College are the unclaimed bodies from the Campbell Medical School and Hospital where the majority of the patients come from the poor classes. Mahamedans take a fair proportion of meat in their diet, but no Mahamedan subjects are available for observation. So most of the subjects observed are adult Hindus including Bengalis, Beharis and Uriyas, who subsist on bulky carbohydrate food.

METHOD OF PRESERVATION ADOPTED

Shortly after death these bodies are injected with 8 ozs. of formaline each and after 24 hours they are injected with a solution of arsenic; except this preliminary injection no fresh formaline has been used locally to harden any portion of the gastro-intestinal tract.

STOMACH

Capacity of the Stomach

In Table A the stomachs of both males and females have been arranged in order of increasing capacity. The capacity has been estimated by distending the stomach with water and measuring the amount. The table shows that the capacity is very variable ranging from 8 oz. to 180 oz. giving an average of about 71½ oz. Those cases in which a definite gross pathological condition was observed in the stomach have been excluded from this table. In Cunningham's *Text Book of Anatomy* the average capacity of the stomach is given as 50 oz. Thus the average capacity of an Indian stomach is much larger

than that observed by Cunningham. In 39 out of the 65 cases (60 per cent.) the capacity is more than 50 oz. In Morris' *Treatise on Anatomy* the average capacity is described as between 1 and 2 litres (about 35 to 70 oz.); compared with that standard also the capacity of an Indian stomach is much larger, as one may expect from a bulky carbohydrate diet.

Table A. *Stomach of both sexes arranged in order of increasing capacity*

No.	Sex	Length in inches	Greatest width in inches	Capacity in ounces
(1)	M	7	3½	8
(2)	M	6	2½	11
(3)	F	6	4	11
(4)	F	5	3½	12
(5)	M	6	5½	16
(6)	F	9½	5	19
(7)	F	8	4	20
(8)	F	9½	5	20
(9)	F	10	3	21
(10)	M	9	4	21
(11)	M	9	3¾	24
(12)	F	9	4	32
(13)	F	9	7	32
(14)	F	9	4	32
(15)	F	9	5½	37
(16)	F	10	6	38
(17)	M	12	4½	38
(18)	F	11	3	40
(19)	M	8½	5½	40
(20)	M	10	7	40
(21)	M	8½	6½	40
(22)	F	9	4½	44
(23)	F	12	5	45
(24)	M	13	4¾	45
(25)	F	13	8	50
(26)	M	13	5	50
(27)	F	13	9	56
(28)	M	12	4	60
(29)	F	10	6	60
(30)	F	10	5	60
(31)	F	11½	7	62
(32)	M	12	5	64
(33)	F	12	5	64
(34)	M	11	7	68
(35)	M	10½	5¼	69
(36)	F	12	6	72
(37)	M	9	6	78
(38)	M	10	6	80
(39)	F	12	7	80
(40)	M	10	6½	80
(41)	M	10	5	80
(42)	F	12	6	80
(43)	M	12	6	80
(44)	M	12	7	85
(45)	M	10	6	88
(46)	M	13	7½	95
(47)	F	21	5	96
(48)	M	12	9½	96
(49)	M	13	7	98
(50)	F	13	8¾	100
(51)	F	11	5	100
(52)	M	11	5	115
(53)	M	12	6	120
(54)	M	15	7	120
(55)	M	15	8½	124
(56)	M	12	5	130
(57)	M	15	11½	132
(58)	M	12	5	135
(59)	M	12	9	136
(60)	F	11¼	5	140
(61)	M	15	9	142
(62)	M	13	7½	144
(63)	F	12½	6½	144
(64)	M	26	6½	152
(65)	F	15	10	180

Table B. *Females only*

No.	Length in inches	Greatest width in inches	Capacity in ounces
(1)	6	4	11
(2)	5	3½	12
(3)	9½	5	19
(4)	8	4	20
(5)	9½	5	20
(6)	10	3	21
(7)	9	4	32
(8)	9	7	32
(9)	9	4	32
(10)	9	5½	37
(11)	10	6	38
(12)	11	3	40
(13)	9	4½	44
(14)	12	5	45
(15)	13	8	50
(16)	13	9	56
(17)	10	6	60
(18)	10	5	60
(19)	11½	7	62
(20)	12	5	64
(21)	12	6	72
(22)	12	7	80
(23)	12	6	80
(24)	21	5	96
(25)	13	8¾	100
(26)	11	5	100
(27)	11¼	5	140
(28)	12½	6½	144
(29)	15	10	180

In Table B female stomachs have been arranged in order of increasing capacity. There are altogether 29 subjects and the capacity ranges from 11 to 180 oz., giving an average of about 60 oz., showing that the capacity of the stomach tends to be smaller in females than in males on an average, though the highest record (viz. 180 oz.) has been in a female stomach. Here again the average capacity (60 oz.) exceeds the average capacity of 50 oz. put down in Cunningham's book.

Table C. *Males only*

No.	Length in inches	Greatest width in inches	Capacity in ounces	No.	Length in inches	Greatest width in inches	Capacity in ounces
(1)	7	3½	8	(19)	10	5	80
(2)	6	2½	11	(20)	12	6	80
(3)	6	5½	16	(21)	12	7	85
(4)	9	4	21	(22)	10	6	88
(5)	9	3¾	24	(23)	13	7½	95
(6)	12	4½	38	(24)	12	9½	96
(7)	8½	5½	40	(25)	13	7	98
(8)	10	7	40	(26)	11	5	115
(9)	8½	6½	40	(27)	12	6	120
(10)	13	4¾	45	(28)	15	7	120
(11)	13	5	50	(29)	15	8½	124
(12)	12	4	60	(30)	12	5	130
(13)	12	5	64	(31)	15	11½	132
(14)	11	7	68	(32)	12	5	135
(15)	10½	5½	69	(33)	12	9	136
(16)	9	6	78	(34)	15	9	142
(17)	10	6	80	(35)	13	7½	144
(18)	10	6½	80	(36)	26	6½	152

In Table C stomachs of male subjects have been arranged in order of increasing capacity. In 36 cases observed the capacity ranges from 8 oz. to 152 oz., giving an average of about 80½ oz., showing that the average capacity of a male stomach is larger than that of the female.

If further observations confirm these results I shall attempt to explain the cause of this sexual difference in the capacity of the stomach. The next question is whether this greater capacity of the stomach in the adult is acquired by accommodating bulky carbohydrate food or whether a bigger capacity is inherited and as such observable in a full term foetus at birth. To ascertain this I observed the capacity of the stomach in a few still born full term foetuses. As it is difficult to procure a sufficient number of them I am not in a position to make any definite statement now, but from the few cases I could get I can predict that a bigger capacity of the stomach is inherited by the Indians, thus supporting the general principle that acquired things are usually transmitted to posterity.

Measurements of the Stomach

Table A shows the measurements of the stomach in both male and female subjects. In taking the measurements the stomach has been moderately distended and the length has been measured in a straight line between two farthest points at the fundal end and the pyloric end. The greatest width

has been obtained by an almost horizontal line (the stomach being placed in anatomical position) usually below the cardiac orifice. It will be observed from Table A that the length varies considerably from 5 to 26 inches, giving an average of 11·25 inches in both sexes taken together. In Cunningham's book the average length is recorded as 10 to 11 inches, whereas in Indians the average is above 11 inches. Taking the average of female subjects (Table B) the length is about 11 inches, whereas the average length in male subjects (Table C) is about 11½ inches. The greatest width varies from 3½ to 11½ inches and on an average is 5·8 inches in both males and females taken together (Table A). The average greatest width according to Buchanan is 5 inches. According to Cunningham the average greatest diameter of the stomach (which is somewhat less than the greatest width) is 4 to 4½ inches. Thus the width in an Indian stomach is considerably greater. Taking the average of female subjects (Table B) the greatest width is about 5·6 inches whereas in male subjects (Table C) it is about 6 inches. Thus the average measurements of an Indian stomach, both length and breadth, are comparatively greater, the increment in breadth being rather more marked. The relation of length and greatest breadth to capacity is not constant as the changes in breadth from the line of greatest measurement are in some cases abrupt and in others more gradual.

Table D. *Female subjects*

No.	Length of Duodenum in inches	Length of Jej. and Ileum in feet	Length of V. appendix in inches	No. of Peyer's patches	Meso-coecum	Ascending Mesocolon	Descending Mesocolon
(1)	7	12	3	14	Nil	Nil	Nil
(2)	6	11	2¾	5	,,	,,	,,
(3)	8	14	1½	25	,,	,,	,,
(4)	9	23½	2	11	,,	,,	,,
(5)	9	14	1½	22	,,	,,	,,
(6)	9½	19¾	2¼	23	,,	,,	,,
(7)	10	21½	3½	26	,,	,,	,,
(8)	6	20	2½	22	,,	,,	,,
(9)	8	22¼	2	28	,,	,,	,,
(10)	9	23	1½	13	,,	,,	,,
(11)	10	24¾	1	22	,,	,,	,,
(12)	9	18	2½	25	,,	,,	,,
(13)	14	24¼	3½	8	,,	,,	Present
(14)	9	19½	2¼	26	Present	Present	,,
(15)	12	23	2	25	Nil	Nil	Nil
(16)	9	23	2	26	,,	,,	,,
(17)	8½	21	1½	17	,,	,,	,,
(18)	10	21½	1¾	48	,,	,,	,,
(19)	11	26	1½	26	,,	,,	,,
(20)	9½	25	3½	31	,,	Present	Present
(21)	9	27	2½	13	,,	Nil	Nil
(22)	9	21	2¼	35	Present	Present	Present
(23)	8	19	3	27	Nil	Nil	Nil
(24)	10	18	1½	30	,,	,,	,,
(25)	9½	29½	4¾	11	,,	,,	,,
(26)	10	21	3	32	Present	Present	Present
(27)	11	23¼	4½	21	Nil	Nil	Nil
(28)	15	29¼	4	10	,,	,,	,,
(29)	11	24	2½	0	,,	,,	,,

Table E. ***Male subjects***

No.	Length of Duodenum in inches	Length of Jej. and Ileum in feet	Length of V. appendix in inches	No. of Peyer's patches	Meso-coecum	Ascending Mesocolon	Descending Mesocolon
(1)	8	17¼	1¾	14	Present	Present	Present
(2)	9	20	3	39	,,	,,	Nil
(3)	10	20	2½	20	,,	,,	Present
(4)	10	27	3½	36	,,	Nil	,,
(5)	9½	22½	3½	25	Nil	,,	Nil
(6)	9	17	3	20	,,	,,	,,
(7)	9	20¼	2¼	34	,,	,,	,,
(8)	10	21	3	15	,,	,,	,,
(9)	9	20	3	27	,,	,,	,,
(10)	9	18½	3½	24	,,	,,	,,
(11)	9	16¾	3	18	Present	Present	Present
(12)	7	20	3	25	Nil	Nil	Nil
(13)	9½	25	3½	31	,,	Present	Present
(14)	14	18	¾	28	,,	Nil	Nil
(15)	9½	22	2½	12	,,	,,	,,
(16)	7¾	14	4	24	,,	,,	,,
(17)	10	21¾	1¾	17	,,	,,	Present
(18)	8	14¼	2½	26	,,	,,	Nil
(19)	8	23½	3	24	,,	,,	,,
(20)	9	23½	3½	12	,,	,,	Present
(21)	10	19½	3	20	,,	,,	Nil
(22)	10	16	2½	20	,,	,,	,,
(23)	11½	17½	1½	28	,,	,,	,,
(24)	10	20	4	25	,,	,,	,,
(25)	12	22	2¾	29	Present	Present	Present
(26)	9	21	2½	33	Nil	Nil	Nil
(27)	10½	22½	2	16	,,	,,	,,
(28)	9½	25	2½	37	,,	Present	Present
(29)	10	25	4	12	,,	Nil	Nil
(30)	9	20	2½	25	,,	,,	,,
(31)	11½	26	3½	21	,,	,,	,,
(32)	10	21	2½	31	,,	,,	,,
(33)	10	22½	3	25	,,	,,	,,
(34)	10½	21½	1½	25	,,	,,	,,
(35)	12	22¼	2½	8	,,	,,	,,
(36)	10	22	1½	27	,,	,,	,,

Duodenum

Observations have been made in 29 female subjects (Table D) and 36 male subjects (Table E). In both sexes taken together the length varies from 6 to 15 inches, giving an average of about 9½ inches. There is not much sexual difference as regards the average length. According to Gray the average length is 10 inches; according to Buchanan 10 to 11 inches; and according to Cunningham 11 inches. Thus in Indians the average length of the duodenum is less.

Length of Jejunum and Ileum

Observations were made in 29 female and 36 male subjects (Tables D and E). Taken together the length varies from 11 feet to 29½ feet giving an average of about 21 feet. This together with 9½ inches the average length of duodenum found in the same subjects gives 21 feet 9½ inches as the average length of the small intestine. According to Treves the average length is 22½ feet in males, 23 feet in females; according to Jonnesco the average in

both sexes is 24 feet 7 inches; according to Buchanan 23 feet; according to Gray 22¾ feet; according to Morris 23 feet; while Cunningham gives the average as over 20 feet. So according to most of the authorities the average length is 22½ to 23 feet. In Indians the average length is less. Taking the male and female subjects separately the average length in females is greater than that of males by about ½ foot thus confirming the observations of Treves.

Aggregated lymph nodules (Peyer's Patches)

The number of aggregated lymph nodules has been noted in the same 65 subjects (Tables D and E). The number varies from nil to 48 giving an average of about 23. According to Gray and Morris the average number is 20 to 30. Buchanan gives the average as 30 and Cunningham gives the average as 30 to 40. So the average here approaches the estimates of Gray and Morris.

Vermiform appendix

The length of the V. appendix has been measured in the same 65 subjects (Tables D and E). The length varies from ¾ inch to 4¾ inches, giving an average of about 2½ inches in both sexes taken together. According to Morris the length varies from ⅘ inch to 10 inches with an average of 3½ to 4 inches. According to Gray the length varies from ⅘ inch to 8 inches with an average of 3¾ inches. According to Berry it varies from ¾ inch to 9 inches with an average of 3½ inches. According to Buchanan it varies from 2 to 6 inches or more. S. Rutherford Macphail of Derby Mental Hospital in his note on the length of the vermiform process in 220 consecutive post mortem examinations (*Journ. of Anatomy*, Part III, April 1917) gives 3·97 inches as the average of males and females taken together. The shortest appendix examined by him was 1 inch and the longest 7½ inches. Thus the average length of the vermiform appendix is much less in Indians and the greatest length has not exceeded 4¾ inches while most of the authorities have observed it as long as 8 to 10 inches. The average length in both the sexes is almost the same.

Mesocoecum

Out of 65 cases (Tables D and E) a mesocoecum has been found in 9, i.e. in about 14 per cent. of both sexes taken together. Taken separately it is present in about 10·3 per cent. of female subjects and in about 17 per cent. of male subjects.

Ascending Mesocolon

Out of 65 cases (Tables D and E) ascending mesocolon has been found in 11, i.e. in about 17 per cent. of both sexes taken together. Taken separately it is present in about 14 per cent. of female subjects and in about 19·4 per cent. of male subjects. Treves found it in 26 per cent. of cases out of 100 cases observed.

Descending Mesocolon

Out of 65 cases (Tables D and E) descending mesocolon has been found in 14 cases, i.e. in about 21·5 per cent. of both sexes taken together. Taken separately it is present in about 17 per cent. of females and 25 per cent. of males. Treves found it in 36 per cent. of cases out of 100 cases observed. Lessaft found a descending mesocolon in about 16 per cent. of cases.

Large Intestine

My observations on this portion of the intestinal canal have not yet been completed and will form the subject of a future communication.

Before concluding I thank my assistants, especially Dr Nagendra Nath Chatterjee, Assistant Professor of Anatomy, for their kind help and co-operation in carrying out these observations.

OBITUARY NOTICE

A. M. PATERSON, M.D. (EDIN.), F.R.C.S. (ENG.)
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BY the death of Professor A. M. PATERSON the Anatomical Society has lost one of its most distinguished and active members.

ANDREW MELVILLE PATERSON

Born at Manchester in 1862 the son of a Presbyterian minister Paterson was early destined for the medical profession following in the footsteps of a long line of ancestors. Receiving his general education at the Manchester Grammar School he proceeded for a short period to the Owens College, Manchester, and thence to the University of Edinburgh where he completed

his curriculum, graduating M.B., C.M. in 1883 with first class honours. Shortly after qualification he was appointed a Junior Demonstrator of Anatomy in the University of Edinburgh, a post which he vacated on being invited by Professor Morrison Watson to return to the Owens College, as his assistant. Professor Paterson has told the writer of the trepidation with which he entered the dread presence of the late Sir William Turner to inform him that he intended resigning in order to accept the Manchester appointment. Great as was Paterson's courage, he would have quailed at the prospect had it not been that he was able to assure Sir William that he had obtained a very competent successor in Arthur Robinson, now the distinguished occupant of the Edinburgh Chair. While at Manchester Paterson had conferred upon him by the University of Edinburgh the degree of Doctor of Medicine together with the award of a Gold Medal for a thesis on the Spinal Nervous System of Mammalia. In 1888 he was appointed to the Chair of Anatomy in University College, Dundee, being the first to occupy that position. He had therefore in Dundee ample opportunity to exercise his undoubted gift for organisation and for arranging departmental accommodation, an opportunity of which he fully availed himself. The Anatomical Department at Dundee will long bear the impress of his hand.

The same year that Paterson went to Dundee, Professor Morrison Watson died, an event which Paterson to the day of his death never ceased to lament for he was a man whose affection was unusually strong and deep.

It was, I believe, while in Dundee that Professor Paterson married Miss Beatrice Eadson and that his singularly happy home life began. How warmly he was devoted to his family and his family to him was much appreciated by those who had the privilege of entering his home circle.

In 1894 he was in succession to Dr Mitchell Banks elected to the Chair of Anatomy at Liverpool, a position which he occupied with much distinction up to his death. Here again as at Dundee he came to a Department which was in process of change and which offered him great scope for his special gifts and here again he took full advantage of the opportunity. Apart from his work in his department Paterson was very active in University affairs and undertook for some years, 1896 to 1903, the arduous duties of the Dean of the Medical Faculty. In later years he served as Honorary Treasurer of the Liverpool Dental Hospital, displaying his customary energy and enthusiasm in the work. Finally in 1917 at the age of fifty-five he took a commission in the R.A.M.C. rising ultimately to the rank of Lieutenant-Colonel. While in the Army Medical Corps he held the position of Assistant Inspector of Military Orthopaedics and later that of Assistant Inspector, Special Military Surgery, acting as chief of staff to his old friend and colleague Major-General Sir Robert Jones.

He served the Anatomical Society in various capacities, being Secretary for Scotland in 1892, Vice-President 1901–4, and President in the years 1908–10.

The outstanding feature to my mind of Paterson's personality was his tireless energy, an energy altogether too kinetic for the somewhat frail body which it animated. He was seldom, if ever, at rest. He thought rapidly, he formed his judgements rapidly, he wrote rapidly whether in rhyme or prose, he sketched rapidly and moved rapidly. These characteristics had their advantages and their disadvantages. He was pre-eminently one who accomplished things, and he has left in the anatomical department of the University of Liverpool a department which is, in my opinion, second to none in equipment, arrangement, and endowment. On the other hand, his haste sometimes made him appear intolerant, but those who were granted the favour of knowing him more intimately appreciated the fact that there was never anything personal in his criticisms or strictures; it was merely that he was consumed with a desire to get things done. No one I have ever known was less willing to compromise, no one was ever less under the moderating influence of the old maxim—*μηδὲν ἄγαν*.

As an anatomist he did not perhaps quite fulfil the brilliant promise of his early days, a fact which he was not slow to acknowledge, and which he regretfully explained as due to his having allowed himself to become engrossed in administrative duties and in academic and polemical discussions. Still, he has a large number of original, thoughtful, and highly important papers on anatomy to his credit, his contributions to our knowledge of the sternum, the sacrum, and the limb-plexuses being of special value. In addition he found time to write a *Manual of Embryology*, *The Anatomist's Note-book*, and a book on the Peripheral Nerves, the last being published since his death.

During the last few years his energy became almost feverish, a phenomenon attributable in my opinion to the deep anxiety with which he followed the events of the war. With the death of his young and gallant son in the Battle of Jutland, his hold on life seemed to have been sensibly weakened and there was about him a wistful sadness which readily won our silent sympathy.

Paterson was a man of cheerful and genial disposition with a great capacity for social enjoyment. It was characteristic of him that in the days when he occupied the President's Chair of the Anatomical Society he should have endeavoured to bring the members of the Society into even more cordial and friendly relationship by inaugurating a small social gathering at the close of each meeting.

Finally, no mention of Paterson would be anything but incomplete which did not refer to the warm generosity which he showed for any cause in which his interest and sympathy had been enlisted. His heart beat in unison with the great heart of Humanity. Altogether he was a man who inspired warm and lasting affection, and he will be long and deeply mourned by an unusually large circle of friends.

VALE.

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